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RANGE RELATIONSHIPS AND DEMOGRAPHY OF FALLOW AND AXIS DEER ON POINT REYES NATIONAL SEASHORE [1]

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Axis and fallow deer on Point Reyes Peninsula, California, have benefited from vegetative changes associated with livestock grazing. Both species preferred areas used by livestock and had similar diets of mostly grassland species. Dietary protein levels were adequate during the dry season, when protein levels of most plants were lowest. The axis deer population has increased considerably faster than the fallow deer population since their introductions in the 1940's. Since litter size, longevity, and food habits do not differ appreciably, it is suggested that this difference results largely from a lower age at first reproduction in the axis deer. The population control program of the National Park Service had decreased the axis deer population as of our last censuses in 1977. However, the fallow deer population continued to increase somewhat at that time due to the absence of control of part of the population.

INTRODUCTION

Naturalized populations of axis deer, *Axis axis axis*, and fallow deer, *Dama dama dama*, have existed on Point Reyes Peninsula for over 3 decades. These populations originated from introductions in the 1940's by Dr. Millard Ottinger, who obtained surplus deer from the San Francisco Zoo and released them at his ranch on Inverness Ridge. Bucks were occasionally shot by local ranchers beginning about 1956, but no population control existed until 1967. In that year, ranchers began shooting both sexes of these deer to limit what they perceived to be competition with their cattle. Hunting was closed on much of Point Reyes Peninsula in late 1971 by the National Park Service following land acquisition for most of Point Reyes National Seashore.

In 1972, we began to study the range relationships and demographic status of these exotic deer. As a result of initial findings of the study, the National Park Service and the California Department of Fish and Game began regular scientific collections of both species in late 1973. Population control and collection of additional information were the objectives. Annual herd reductions have continued in an attempt to prevent further population growth. This paper compares the range relationships and demography of axis and fallow deer on Point Reyes Peninsula, and assesses the success of the population reduction program.

STUDY AREA

Point Reyes Peninsula is located in Marin County, California. It is bounded on the west by the San Andreas Fault, which forms the rift through Tomales Bay and Olema Valley (Figure 1).

The region is a Mediterranean type ecosystem with a mesothermal climate (Di Castri and Mooney 1973). Most precipitation is in the form of rain occurring from November through April. A 63-year annual rainfall average for the Point Reyes Lighthouse was 48.3 cm as reported by the U.S. Weather Bureau (1943).
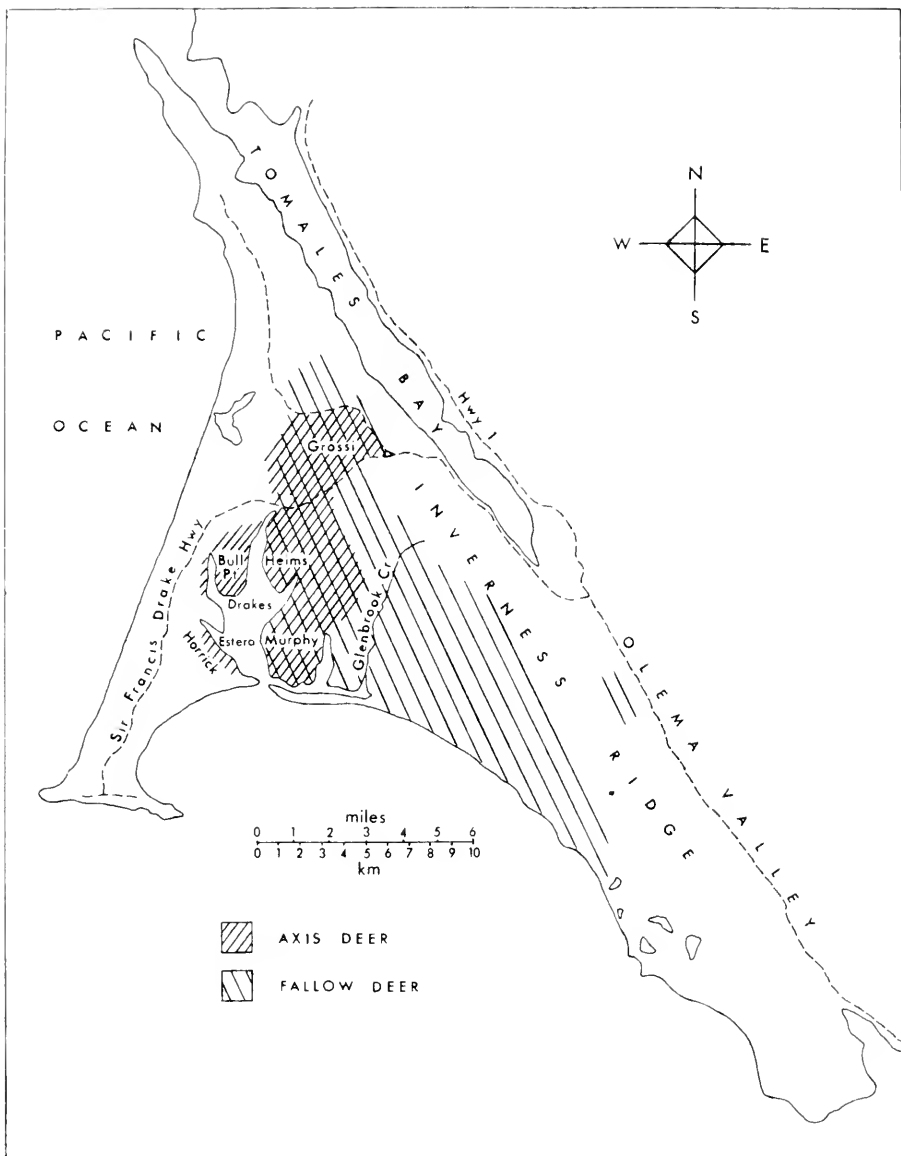
FIGURE 1.   Ranges of the fallow and axis deer on Point Reyes National Seashore. Cattle grazing occurs in the western and northern part of the National Seashore; its eastern boundary coincides with that of the axis deer range. Names of locations refer to family names associated with ranches.

Precipitation also occurs in the form of advection fog, particularly in summer. This fog, as well as frequent wind, emanates from the Pacific Ocean, which has a considerable effect on the temperature of Point Reyes Peninsula. The 60-yr mean January temperature at the Lighthouse was 9.8° C, while the mean July temperature was 12.1° C as reported by the U.S. Weather Bureau (1941).

The cool temperature and moist fog have a marked influence on the vegetation of Point Reyes Peninsula. The study area grassland is perennial, in contrast to annual grasslands found just inland. The prevailing brush type is northern coastal scrub (Munz and Keck 1949), as compared with drier inland slopes where chaparral predominates. Coyote brush, *Baccharis pilularis consanguinea,* is an important constitutent of all scrub communities in the exotic deer range, while other woody species are highly variable in their abundance. Other important species are California sagebrush, *Artemisia californica;* sword fern, *Polystichum munitum;* bush monkeyflower, *Mimulus aurantiacus;* blackberry, *Rubus vitifolius;* thimbleberry, *R. parviflorus;* coffeeberry, *Rhamnus californica;* and blue brush, *Ceanothus thyrsiflorus.*

Large areas of scrub cover on Point Reyes Peninsula have been converted to grazable grassland through bulldozing, burning, plowing, and seeding. Brush is generally limited to slopes too steep for bulldozing. This condition is maintained through continuous livestock grazing and periodic plowing and reseeding on the northern half of Point Reyes Peninsula, where livestock operations continue under lease arrangements.

The grasslands are composed of a mosaic of dominant species that vary with soil type, soil moisture, and successional stage. Important grasses are perennial ryegrass, *Lolium perenne;* oatgrass, *Danthonia californica;* hairgrass, *Deschampsia caespitosa* ssp. holciformis; annual fescue, *Festuca dertonensis;* silver hairgrass, *Aira caryophyllea;* soft chess, *Bromus mollis;* ripgut, *B. diandrus;* and velvet grass, *Holcus lanatus.* Species of clover, *Trifolium* spp., and bur clover, *Medicago hispida,* are also abundant on some pastures in spring. Most grass and clover species dry up in the summer, while broad-leaved forb species, notably hairy cat's ear, *Hypochoeris radicata;* ribwort, *Plantago lanceolata;* and bird's foot trefoil, *Lotus corniculatus,* remain green. Low growing broad-leaved forbs are notably lacking in ungrazed grasslands. Bull thistle, *Cirsium vulgare;* and milk thistle, *Silybum marianum,* are present in all grasslands.

Native columbian black-tailed deer, *Odocoileus hemionus columbianus,* are found throughout Point Reyes Peninsula.

METHODS

Observations of deer were made with 7X binoculars and 20X, 25X, or 15–60X spotting scopes. The diurnal habits, preference for open land, and conspicuous large herds of both exotic deer species make direct census feasible. Largest group sizes for axis deer were observed during pasture growth from October through May, with a maximum of 200 in a group. Fallow deer exhibit peak group sizes in summer and winter, separated by fawning in spring and the rut in the fall. The maximum herd size recorded for fallow deer was 103. Population censuses were made during seasons of maximum herding for each species, as this was found to provide the most complete counts. Several total counts were made during each census, from which the most complete was chosen. Critical to success of censuses was prior knowledge of the patches of habitat used by the deer throughout their ranges.

Double counting during censuses was avoided by taking caution not to cause deer to flee into uncensused areas and recognition of groups by size and composition. The four color types of fallow deer present on Point Reyes Peninsula

(white, black, common, and menil; see Cadman 1966 for descriptions) aided in recognition of groups. The range of each species was broken into units that could be censused in 1 day. For the axis deer, these areas (labelled Grossi, Heims, Murphy, Horrick, and Bull Point on Figure 1) had only occasional animal interchange, which greatly reduced the possibility of duplicate counting. The more continuous distribution of the fallow deer makes division of their range (by Sir Francis Drake Highway and Glenbrook Creek; see Figure 1) more arbitrary. Nevertheless, movement across Sir Francis Drake Highway is rare, and day to day identification of groups through sex, age, and color composition, as well as through individual recognition of the majority of the bucks, greatly reduced the probability of duplicating counts. Census data for each species were considered acceptable only if the entire range (excepting Bull Point and the Horrick Ranch of the axis deer range) was covered within a few days under favorable conditions. A helicopter was used in the 1975–76 and 1977 censuses. Only the 1977 helicopter count of fallow deer recorded more deer than ground counts, and was used as a total population estimate. Sex and age composition of both species was obtained only during ground counts.

Data on plant species in the diets were obtained by direct observation of feeding deer and through inspection of plants at feeding sites. Rumen contents from deer collected between 1973 and 1975 were identified by the Wildlife Investigations Laboratory of the California Department of Fish and Game.

Monthly samples of selected forage species from the Heims Ranch area and rumen samples from late summer of 1972 were analyzed for protein content as a measure of nutritional quality. Rumen samples were analyzed for protein content after washing with water in an attempt to remove urea, mucin, and microbial sources of nitrogen (Klein 1962). All protein analysis was by the Kjeldahl method on samples oven-dried at 70° C and ground through a 40-mesh screen.

Botanical nomenclature throughout this paper follows Munz (1959, 1968).

RESULTS
Range Relationships

The literature on habitat and forage preferences of both axis and fallow deer stresses the importance of grassland vegetation (Batcheler 1960, Cadman 1966, Schaller 1967, Ueckermann and Hansen 1968, Chapman and Chapman 1975, Smith 1977). Both exotic deer species on Point Reyes Peninsula were observed to feed exclusively on grassland species during the pasture growing season. During this period, the vegetation is at its maximum nutritional value on a dry weight basis (Table 1). In April and May, as grasses and forbs flowered and produced seed, their protein levels dropped, and the fallow and axis deer became increasingly selective in their feeding. Protein levels of grasses continued to decrease after they dried up in early summer, and dropped below the 6–7% maintenance level for deer (Dietz 1965) in early autumn following the leaching action of the early first fall rains in 1972 (Table 1). Forb species that continued to grow and flower through the summer maintained higher protein levels than grasses. These became the sought-after forage items of the exotic deer during summer, particularly the flower heads of hairy cat's ear and the leaves and flowers of bird's foot trefoil and ribwort.

TABLE 1. Seasonal Changes in Protein Content (dry weight percentages) of Selected Forage Species Collected in 1972–1973. The 1 Oct. Collection of Grasses Consisted of Dried Seed Heads with Stems of the Previous Season's Growth. Grasses from 15 Nov. through 12 May Were Green Leaves. Grasses from 3 June through 9 Aug. Were Seed Heads with Stems.

Forage species					Collection date					
Grasses	1 Oct.	15 Nov.	3 Dec.	21 Jan.	25 Feb.	1 Apr.	12 May	3 June	3 July	9 Aug.
Lolium perenne................	6.2	20.0	23.8	23.7	25.0	22.0	9.4	10.3	6.9	6.6
Bromus mollis	5.4	14.0	8.2	20.4	19.6	15.5	9.8	11.6	8.5	7.3
Festuca dertonensis	3.8	13.0	–	14.0	12.6	9.4	10.0	8.4	7.8	5.0
Forbs										
Plantago lanceolata (leaves)	12.1	19.4	21.2	22.6	24.4	16.6	14.0	11.1	9.9	6.7
P. lanceolata (seed heads).....................	9.6	–	–	–	–	–	12.2	10.5	8.0	9.9
Hypochoeris radicata (leaves)	–	–	–	19.6	21.8	16.2	14.4	11.6	8.2	9.6
H. radicata (flowers)	15.8	14.6	–	–	–	–	13.5	13.9	12.6	12.8
Lotus corniculatus............	–	23.6	25.1	25.2	27.3	26.0	20.7	19.3	17.2	17.7
Browse										
Rubus vitifolius	8.9	11.6	9.7	13.2	18.2	16.3	15.3	14.4	10.2	8.5
Cytisus scoparius	15.4	23.4	28.4	22.3	26.9	24.2	25.8	21.7	20.2	20.6
Myrica californica............	–	9.2	9.6	10.0	10.4	10.9	17.3	15.4	12.3	10.8

Rumen analyses substantiated the shift to forbs in summer. The native perennial oatgrass remained green throughout the year, as did perennial ryegrass; harding grass, *Phalaris tuberosa*; orchard grass, *Dactylis glomerata*; and alta fescue, *F. arundinacea*, in occasional localized spots. Patches of these green grasses received noticeably closer grazing in summer than surrounding species, and undoubtedly accounted for much of the grass in summer rumen samples (Table 2).

TABLE 2. Summary of Rumen Contents of Fallow and Axis Deer Collected on Point Reyes Peninsula, 1973–1975. Values are Percent Volume. Analysis Was by the California Department of Fish and Game Wildlife Investigations Lab.

Species	Season	% Grass	% Forbs	% Browse	Sample size [1]
fallow................................	winter	97.3	2.7	0.0	30
	spring	70.2	28.5	1.3	22
	summer	30.3	69.6	0.1	20
	fall	69.1	30.3	0.5	20
axis......................................	winter	99.0	0.7	0.3	32
	spring	89.5	9.9	0.6	20
	summer	48.3	50.3	1.4	27
	fall	79.0	19.6	1.3	22

[1] number of rumen samples

Milk and bull thistles were eaten by both exotic deer species during summer, as were some browse species, notably Scotch broom, *Cytisus scoparius*; blackberry; and poison hemlock, *Conium maculatum*; axis deer also browsed wax myrtle, *Myrica californica*. Overall, browse constituted a small fraction of the diet (Table 2).

In late summer and early autumn, before rains initiated fresh pasture growth, both quantity and nutritional quality of the forage were at a minimum for the exotic deer on Point Reyes Peninsula. This should have constituted the period

of lowest diet quality for the deer. However, high protein levels of washed rumen samples collected in late summer of 1972 suggested no shortage of nutritious forage. The average amount of protein in washed samples was 15% each for fallow and axis deer. This figure approaches the 15–17% found by Verme and Ullrey (1972) to be optimal in a formulated diet for white-tailed deer, *O. virginianus.*

Two land use practices on Point Reyes Peninsula have been beneficial to the exotic deer. First, widespread brush removal has increased the acreage of grass-land habitat. Second, livestock grazing affects the outcome of plant competition for light, favoring the growth of broad-leaved forb species over grasses. These forbs are the preferred forage items of both exotic species during the dry season. Also, livestock grazing reduces rank grasses (wolf plants) to more palatable forage.

Both deer species preferred livestock areas, but to different degrees. Range expansions of axis deer have been solely into livestock areas to the west and north of Drakes Estero (Figure 1). Despite easier accessibility, no expansion has occurred toward the east and southeast, where no livestock are grazed. Fallow deer have also shown a preference for the livestock areas, especially in summer, but their range also includes considerable area ungrazed by livestock. Local residents in areas of continued livestock grazing have noted a shift in distribution of fallow deer away from neighboring areas that are no longer grazed by live-stock.

Life History

Fallow and axis deer differ in their breeding cycles. Fallow deer are seasonal breeders, with the rut occurring largely in October and fawning mostly in June. This is an adaptation to their native temperate climate of the Mediterranean region of Europe and Asia Minor (Whitehead 1972). In contrast, axis deer breed throughout the year, which is considered to be a consequence of their native tropical climate in India (Schaller 1967). However, peak fawning periods have been recorded for axis deer in India (Schaller 1967), as well as in introduced populations in Hawaii (Graf and Nichols 1967) and Texas (Russ 1977). Also, the highest percentage of bucks in hard antler has been found to precede the fawning peak by the length of gestation in India (Schaller 1967) and Texas (Fuchs 1977); thus the annual cycle of the percent of bucks in hard antler corresponds with the cycle of breeding activity. Such an antler cycle is conspicu-ous for axis deer on Point Reyes Peninsula (Figure 2). Four censuses of axis deer in winter 1976 yielded a steady rise in the ratio of new fawns (less than 1 month old) to does from 0.11 in early January to 0.24 in early March. This suggests an early spring fawning peak and the same temporal relationship between the antler hardening and fawning peaks evident in other populations.

Population Size and Growth Rates

During the last census (1977), 364 axis deer and a higher than expected total of 523 fallow deer were recorded (Table 3). Previous fallow deer counts appar-ently missed some deer, as a recruitment rate approximately double that record-ed for the 1975 fawn crop would have been necessary to explain the 1977 total. All axis deer censuses reported in Table 3 are believed to be accurate due to the relatively small area censused.
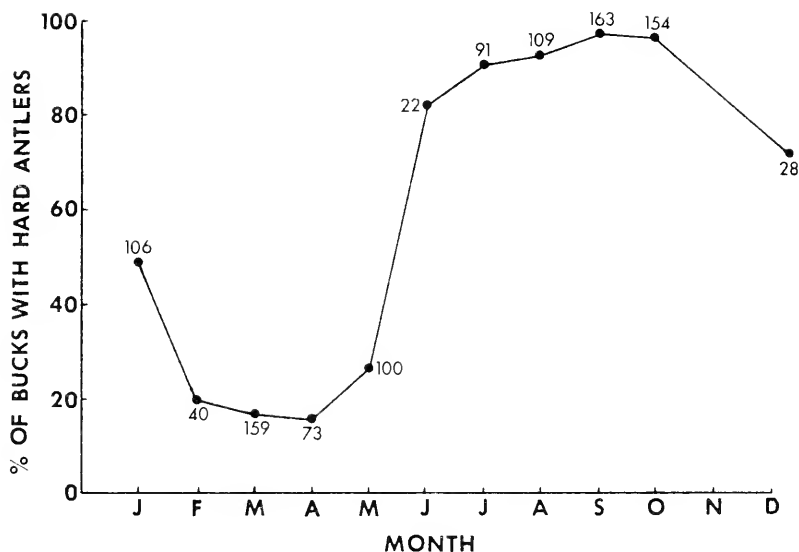
FIGURE 2.   Antler cycle of axis deer on Point Reyes Peninsula. Data points are composited for 1972 and 1973. Sample sizes are adjacent to data points.

TABLE 3.   **Total Numbers and Sex-age Ratios of Axis and Fallow Deer Recorded in Censuses on Point Reyes Peninsula. All Censuses Were Made from the Ground except the March 1977 Fallow Deer Count, Which Was Made from a Helicopter. See Figure 1 for Area Designations.**

Fallow Deer	*Dec. 1973*	*Dec. 1975*	*March 1977*
North of Sir Francis Drake Highway	47	47	54
Sir Francis Drake Highway to Glenbrook Creek...........................	270	228	163
South of Glenbrook Creek..	149	206	283
Olema Valley..	4	12	23
Total	470	493	523
Fawns:Does:Bucks...	46:100:42	40:100:58	46:100:43 *
Axis deer	*Oct. 1973*	*March 1976*	*May 1977*
Grossi...	168	300	252
Heims..	164	70	39
Murphy...	59	59	28
Bull Point	5	29	45
Horrick	11	3	0
Total	407	461	364
Fawns:Does:Bucks...	66:100:56	75:100:73	55:100:57

* derived from three ground censuses.

Calculations of population growth rates were made for intervals between censuses and between introductions and censuses; thus a range of growth rate values was produced. Growth rate equations have incorporated hunting mortality as a separate variable in order to estimate "intrinsic" growth rates in the absence of hunting. Also, calculations involved only females, because they are

the reproductive unit of the population and hunting by ranchers in the late 1960's was directed toward does to control the population. This bias in hunting mortality would produce misleading results if the population as a whole were used to calculate growth rates.

Because the 1977 fallow deer helicopter count represented a change in census method, no growth rate calculations were made for the intervals between that census and the previous ones. However, only a relatively small difference exists between results involving the 1977 count and previous counts, when long term calculations were made for the intervals beginning with introductions in 1942 (Table 4). For the axis deer, only one calculation for an interval beginning with introductions in 1947 was made, since others necessarily will yield values within the range of axis deer values already present in Table 4.

TABLE 4.   Calculated Annual Percent Increase Rates for Axis and Fallow Deer Female Populations on Point Reyes Peninsula in the Absence of Hunting. Calculation Details are Found in the Appendix.

Species	Interval	Annual percent increase
fallow	1942–1973	11.0
	1942–1977	11.6
	1973–1975	14.6
axis	1947–1973	22.5
	1973–1976	23.5
	1976–1977	20.0

Past records of the San Francisco Zoo are poor, and, except for one instance, do not include sex ratios of deer introduced to Point Reyes Peninsula (Marvin Jones, pers. commun.). Since growth rate calculations are made only for the female segment of the population, those made for intervals beginning with introductions are only as good as the assumptions regarding sex ratios of introductions. Two male and two female axis deer were introduced in 1948. Since only four other axis deer were introduced in 1947, our assumption of an equal sex ratio of axis deer introductions has a high probability of being correct. Twenty-eight fallow deer, sex ratio unknown, were introduced over a period of 12 years (see Appendix); thus the assumed number of does in introductions is highly speculative. However, sensitivity analysis of the growth rate calculations between 1942 and 1977 suggest that changes in these assumptions have relatively little effect on the calculated value. For instance, a change in the assumed number of does in the 1942 introduction from eight, which yields 11.6% annual increase, to seven yields 11.9%, while six and five yield 12.3% and 12.7% respectively. These changes are small compared with the range of values for fallow deer already present (Table 4).

The calculated growth rate of the fallow deer population between 1973 and 1975 is notably higher than for intervals beginning with introductions (Table 4). Unrecorded poaching mortality would have the effect of underestimating the increase rates calculated for the intervals beginning in 1942, since hunting mortality prior to 1973 would be underestimated. Poaching has occurred on Point Reyes Peninsula for many years and has probably had more effect on fallow deer than axis deer due to the greater range of the former.

Fixed growth rates are assumed in calculations as a necessary approximation. Some variation in growth rates due to environmental fluctuations is to be expected, as suggested by variation in fawn:doe ratios during this study (Table 3). Therefore, the ranges of values presented in Table 4 are more meaningful than any single value. The growth rate models have ignored density-dependent influences on population growth rates. The relative closeness of long term and recent short term growth rate values for both species suggest that the influence of density on growth rates is not yet significant. The additional assumption of additivity of hunting and natural mortality is also appropriate for populations at this stage in their growth curves (McCullough 1979).

DISCUSSION

The growth rate of the axis deer population is notably higher than that of the fallow deer. The two species do not differ in their food habits, diet quality, litter size (both single-bearing), or longevity (based on ages of collected deer; Oscar Brunetti, Calif. Dept. Fish and Game, pers. commun.); thus age at first reproduction and breeding frequency of does must account for this difference in growth rates. Due to restrictions of seasonal breeding, fallow does do not normally first conceive until their second breeding season, at approximately 16 months of age (Ueckermann and Hansen 1968), and bear fawns at yearly intervals. In contrast, the year-round breeding of axis deer results in females first conceiving at a variety of ages, depending on nutrition, and makes intervals of less than 1 year between successive conceptions possible. This latter consideration is particularly significant when females lose fawns early, as they need not wait for a yearly breeding season to conceive again (Schaller 1967). Graf and Nichols (1967) reported age at first conception as young as 4 months for axis deer in Hawaii. Data from 2 young axis females shot on Point Reyes Peninsula in 1973 indicated first conception at about 10 months of age, or approximately 6 months earlier than fallow deer. Cole (1954) and Lewontin (1965) demonstrated mathematically the large effects of reduction in age at first reproduction on population growth rates. This factor is probably the main cause of the large difference between axis and fallow deer in the calculated rates of population growth.

Point Reyes National Seashore is classified as a recreation area where management policies do not require the elimination of exotic species. Nevertheless, the National Park Service recognizes the potential danger to natural ecosystems of uncontrolled exotic ungulate populations and seeks to maintain the axis and fallow deer populations at or below the 1973 levels (National Park Service 1976). Data indicate that both populations are in the rapid increase phase near or below the inflection point in the growth curves exhibited by introduced ungulate populations (Caughley 1970). Populations in this general region of the growth curve exhibit the greatest annual productivity (Caughley 1976, McCullough 1979). Thus, sustained herd reduction efforts by the National Park Service will be necessary to maintain the populations at these densities, and assure protection of the vegetation and soils from damage by overgrazing.

As a result of the exotic deer control program at Point Reyes, the axis deer population has been reduced, while the fallow deer population continues to increase slightly (Table 3). Control had not been practiced outside the livestock range or on the Bull Point and Horrick sections of the axis deer population as

of our last census in 1977. Poaching may account for the disappearance of the small axis deer population on the Horrick Ranch. Lack of control of the fallow deer population south of Glenbrook Creek and in the Olema Valley has allowed both population size and area of occupied range to continue expanding. If this trend is allowed to continue, future population control will become increasingly difficult.

ACKNOWLEDGMENTS

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APPENDIX
Population Growth Rate Calculations

Records from the San Francisco Zoo provide the following information on introductions (Marvin Jones, pers. commun.): 15 fallow deer were introduced in 1942, 11 in 1947, and 2 in 1954; 4 axis deer were introduced in 1947 and 4 more (2 male, 2 female) in 1948. Specific information on hunting mortality comes from estimates made by local ranchers and from known mortality associated with herd reduction programs. The following calculations involve only females; female fawns killed during the herd reductions are treated as equivalent to adult does killed the following year.

Axis Deer

Because axis deer exhibit continuous reproduction, a continuous function with instantaneous rates is used to represent their population change.

1947–1973

Two does were introduced in 1948, and of the 4 introduced in 1947, it is most likely that 2 were females, each of which would bear a fawn. Thus it is assumed that 5 does existed in 1948. The October 1973 census yielded 181 does (Table 3). Hunting mortality during the 4 years beginning 1968 was continuous, totaling 235 does; thus it is convenient to assume a constant rate of hunting mortality (h) over this 4 year period, and the population growth equation for the 25 years is

$$181 = 5e^{25r-4h},$$

where r is the instantaneous rate of population increase. Solving for h yields

(1) $h = \dfrac{\ln 5 - \ln 181 + 25r}{4} = 6.25r - 0.897.$

This is subjected to the constraint that the summation of the yearly hunting losses between 1968 and 1971 total 235 does, which may be expressed as

(2) $235 = (5e^{19r} - 5e^{19r-h}) + (5e^{20r-h} - 5e^{20r-2h}) + (5e^{21r-2h} - 5e^{21r-3h}) + (5e^{22r-3h} - 5e^{22r-4h}).$

Substituting equation 1 into equation 2 and simplifying yields

$$47 = (e^{19r} - e^{12.75r + 0.897}) + (e^{13.75r + 0.897} - e^{7.5r + 1.794}) +$$
$$(e^{8.5r + 1.794} - e^{2.25r + 2.691}) + (e^{3.25r + 2.691} - e^{-3r + 3.588}).$$

By the Newton approximation method, $r = 0.203$ has been found to satisfy this equation, which is equivalent to $\lambda = 1.225$, where $\lambda = e^r$ (Mertz 1970), or a 22.5% annual growth rate.

1973–1976

Census results yielded 181 does in October 1973 and 187 does in March 1976 (Table 3). The time interval between censuses is 2.416 years. Forty-one does were removed from the population during the first year and 34 during the second year. Herd reductions were carried out monthly, thus may be regarded as constant mortality rates, and the resultant equation is

(3) $187 = 181\exp^{(2.416r - h_1 - h_2)},$

where h_1 and h_2 represent the first and second of these reductions respectively, and $\exp(x) = e^x$. The equation for the first year's reduction is

$$41 = 181 - 181\exp(-h_1)$$

which yields $h_1 = 0.257$. Similarly, the equation for reduction in the second year is

$$34 = 181\exp(r - h_1) - 181\exp(r - h_1 - h_2),$$

and substituting 0.257 for h_1 yields

$$h_2 = r - 0.257 - \ln(e^{r-0.257} - 0.188).$$

Substitution of these values for h_1 and h_2 into equation 3 yields

$$187 = 181\exp\{2.416r - 0.257 - [(r - 0.257 - l_n (\exp (r - 0.257) - 0.188)]\},$$

which reduces to

$$187 = 181\exp[1.416r + l_n (\exp(r - 0.257) - 0.188)],$$

for which the Newton approximation method yields a solution of $r = 0.211$, which is equivalent to a finite growth rate (λ) of 1.235, or 23.5% annually.

1976–1977

Census results yielded 187 does in March 1976 and 178 does in May 1977 (Table 3). The time interval between censuses is 1.167 years, during which time

43 does were removed from the population. The situation may be represented by the following equations:

(4) $178 = 187e^{1.167(r-h)}$

(5) $43 = 187 - 187e^{-1.167h}$.

The solution to equation 5 is h = 0.224, and substitution of this into equation 4 yields

$$178 = 187e^{1.167r - 0.261},$$

for which r = 0.181 is the solution, and is equivalent to a finite rate of 1.200, or 20.0% annually.

Fallow Deer

Fallow deer reproduction is highly seasonal, with fawning occurring mostly in June. Consequently, a simple model of yearly finite increase rates has been used to calculate rates of population change. Exponents for each term in the equations represent the number of summer fawning seasons between the census and each addition or removal of does. Thus, does shot between September and the time of winter censuses are assigned a zero exponent.

1942-1973

Since no data exist on sex ratios of fallow deer introductions, it is hypothesized that females constituted 8 of the 15 introduced in 1942, 6 of the 11 in 1947 and 1 of the 2 in 1954. Estimated hunting mortality of does is 7 per year for 4 years beginning in 1968, 1 in September 1972 and 6 in the fall of 1973 prior to the December census that counted 250 does (Table 3). This is represented by the equation

$$250 = 8\lambda^{31} + 6\lambda^{26} + \lambda^{18} - 7\lambda^6 - 7\lambda^5 - 7\lambda^4 - 7\lambda^3 - \lambda - 6,$$

which by the Newton approximation method is satisfied by $\lambda = 1.110$ (11.0% annually).

1942-1977

When the 1977 fawn:doe:buck ratio is applied to the total population count in Table 3, the resultant doe population is 277. Thirty-five does were shot during the year beginning in September 1973, 36 the following year, 7 between March and September 1976, and 46 between November 1976 and March 1977. This yields the equation

$$277 = 8\lambda^{34} + 6\lambda^{29} + \lambda^{21} - 7\lambda^9 - 7\lambda^8 - 7\lambda^7 - 7\lambda^6 - \lambda^4 - 35\lambda^3 - 36\lambda^2 - 7\lambda - 46,$$

which is satisfied by $\lambda = 1.116$ (11.6% annually).

1973–1975

The doe counts were 250 in 1973 and 249 in 1975. Twenty-nine does were shot between December 1973 and August 1974 and 36 during the following year. This may be represented by the following equation:

$$249 = 250\lambda^2 - 29\lambda^2 - 36\lambda,$$

which reduces to

$$0 = 221\lambda^2 - 36\lambda - 249,$$

the solution of which is $\lambda = 1.146$ by the quadratic formula, or 14.6% annually.

GROWTH OF ADULT STRIPED BASS IN THE SACRAMENTO-SAN JOAQUIN ESTUARY [1]

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Adult striped bass, *Morone saxatilis,* growth in the Sacramento-San Joaqin Estuary was described well by the von Bertalanffy growth equation. After age 3, females grew more rapidly than males and by age 6 they were as large as 7-yr-old males. The size bass attain as adults appeared to be affected by their growth rate as young-of-the-year. An average 2 cm decrease in adult mean length was associated with an 18% decrease in young bass growth rate commencing in 1970. Annual mean growth in 1971 was substantially higher than for any other year and was associated with abundant forage in San Francisco and San Pablo bays.

INTRODUCTION

Adult striped bass, *Morone saxatilis,* growth in the Sacramento-San Joaquin Estuary from 1969–1978 was studied to identify possible factors affecting growth rates. Documentation of such resource requirements is a prerequisite for rational fishery management decisions. Previous striped bass growth studies (Scofield 1931, Robinson 1960, Miller and Orsi 1969) demonstrated a significant ($P <$ 0.05) increase in mean length for age groups 3 to 7 between the 1920's and 1950's. Robinson (1960) suggested this size increase may have been due to decreased competition resulting from a decline in the striped bass population over this period as indicated by a decreasing trend in catch per unit effort (Chadwick 1962). The size that bass attain as adults might also be influenced by their growth when immature (Merriman 1941, Tiller 1943).

Robinson (1960) observed fluctuations among annual growth increments for 1952 to 1956, but did not have sufficient data to determine either the causes or the significance of these fluctuations.

Specific objectives of my study were to: (i) describe the present age-length relationship of adult striped bass in the estuary, (ii) determine if the size attained as adults is affected by their growth as young-of-the-year, and (iii) determine if fluctuations in annual growth increments are associated with fluctuation in adult bass and/or forage abundance.

A mark-recapture study begun in 1969 to estimate adult striped bass abundance has provided age-length data for fish 3 yr and older during spring, summer, and fall. Annual tow net and midwater trawl surveys in the estuary (Stevens 1977*a*) provided data to calculate growth of young striped bass and to estimate forage abundance.

MATERIALS AND METHODS

Striped bass were captured each year (1969–1978) during their spring spawning migration (mid-March to mid-June). The primary objectives of this work was to capture legal sized [$\geq$ 40.6 cm total length (TL), $\cong$ 38 cm fork length (FL) bass for tagging; therefore, my growth study only includes bass $\geq$ 38 cm FL.

Fish were captured in wire fyke traps (Hallock, Fry, and LaFaunce 1957) in the Sacramento River near Clarksburg and with drift gill nets (stretched mesh sizes: 10.2 cm to 14.0 cm) in the San Joaquin River near Antioch. In 1977 and 1978 fish were captured in the San Joaquin River only. A creel census in the San Francisco Bay area during summer and fall (1969–1977) provided additional monthly samples. Sex and fork length (to the nearest centimetre) were recorded for all fish from which scale samples were collected for aging. During spring, fish were classified as male if milt was extruded when abdominal pressure was applied; if milt did not flow the fish were classified as female. During summer and fall sex was determined by dissection.

Scales were taken midway between the spinous dorsal fin and the lateral line and independently read by two individuals using binocular dissecting microscopes at 30X magnification. Scofield (1931) demonstrated the validity of using scale samples from striped bass to determine age. Scale growth appears as fairly evenly spaced arched circuli lying between numerous radii (Figure 1). Most annuli are very distinct, appearing as thick ridges continuous around the anterior
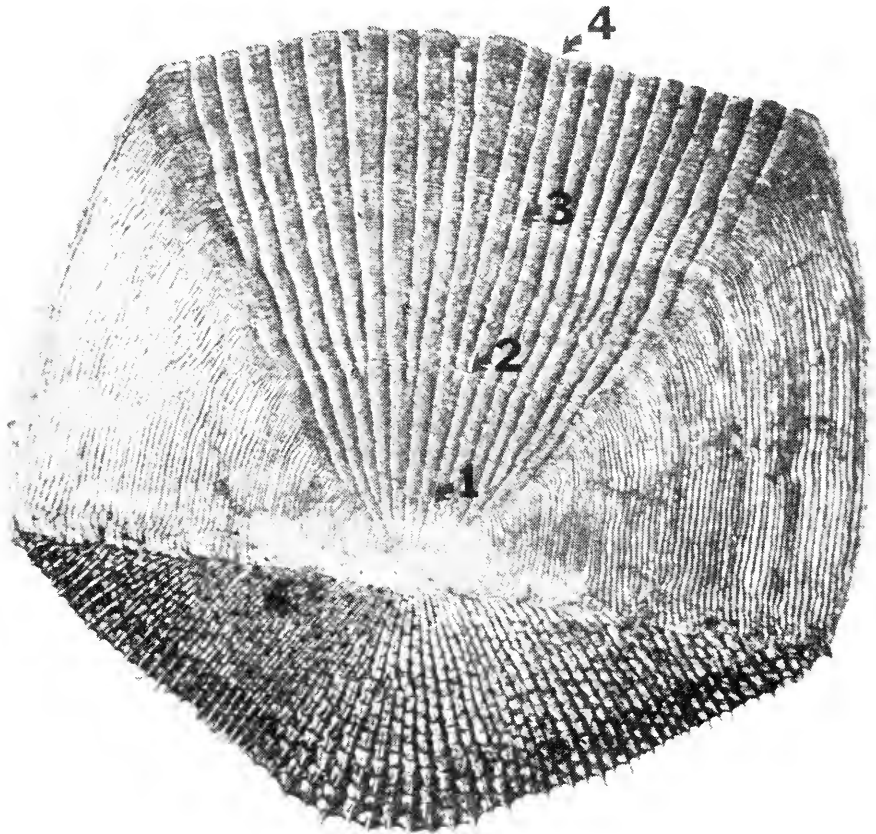

FIGURE 1.   Scale from a 4-yr-old striped bass collected in the spring of 1979 from the Sacramento-San Joaquin Estuary. Marks not labeled are false annuli. *Photograph by Tom Taylor.*

and lateral fields. Annuli tend to bend inward at the base of the lateral field "crossing over" circuli. Since annuli are not visible until normal growth resumes in spring or early summer the scales collected in the spring were assumed to have an annulus at the margin even if one was not detected.

Identification of false or extra annuli is often difficult. False annuli may cover only half the scale, the circuli comprising them are often curved instead of straight, and their spacing is usually irregular. There is an orderly decrease in spacing between true annuli as the fish age.

Among older fish, the annuli become compacted toward the margin making individual annuli very hard to detect. Hence, while ages up to 7 or 8 yr can be readily determined, the incidence of age disagreements between readers increases to over 50% in older bass and ages may be underestimated. The oldest age that we estimated from reading more than 125,000 scales was 19 yr; however, recovery in 1977 of a bass tagged 17 yr earlier when it was 6 or 7-yr-old reveals that bass live to at least age 23.

Average growth from age 3 to 12 was estimated for males and females separately by fitting the mean fork lengths ($\overline{FL}$) observed each spring to the von Bertalanffy growth equation (Ricker 1975) using the least squares computation (Abramson 1971). Bass over 12-yr-old were not included because samples were too small.

Average seasonal growth (May to November) for each sex was estimated for ages 3 to 8. The procedure was: (i) each year determine the mean length of each sex-age group during each month of this period, and (ii) calculate linear regressions of mean lengths on month for each age group. The regression coefficients were estimates of average seasonal growth rates. Monthly samples usually were small for bass over 8-yr-old so seasonal growth rate was not estimated for those fish.

Inspection of age-length data (Tables 1 and 2) suggested that average lengths were smaller for some year classes than for others at all ages; therefore, analysis of variance tests were used to determine if significant differences occurred among mean lengths of individual year classes at the various ages. Student-Newman-Keuls tests, *a posteriori* stepwise range test (Sokal and Rohlf 1969), were used to determine which groups were significantly different. This analysis demonstrated a clear distinction between year classes 1965–1969 and 1970–1975 for both sexes. Therefore, for each age group (3 to 7) grand mean fork lengths were calculated for sexes combined from the mean lengths of the 1965–1969 and the 1970–1975 year classes. Grand mean lengths were used in linear regressions on age to determine if growth rates differed for these two sets of year classes as adults or if the differences observed were solely due to differences in growth in younger stages.

The hypothesis that growth rates of immature striped bass affect the size attained as adults was tested by correlating the annual spring lengths of individual adult age groups with growth rates (mm/day) estimated from July to October for the same year classes as young-of-the-year (Table 3).

TABLE 1. Mean Fork Lengths (cm) ± SD for Male Striped Bass Tagged During Spring in the Sacramento-San Joaquin Estuary.[a]

Year	3[b]	4	5	6	7	8	9
1969	43.6(971) YC = 1966	50.5±5.5(3054) YC = 1965	58.2±5.8(1949) YC = 1964	64.8±5.2(1566) YC = 1963	70.8±6.0(805) YC = 1962	75.8±5.3(577) YC = 1961	79.1±5.1(423) YC = 1960
1970	44.5(986) YC = 1967	50.8±4.8(1692)	58.7±5.2(685)	64.6±5.1(338)	70.1±5.1(295)	75.2±4.8(141)	78.5±4.2(82)
1971	43.1(1105) YC = 1968	50.5±5.0(3069)	58.3±5.2(1123)	65.2±5.2(368)	70.4±4.5(206)	74.2±4.5(229)	77.8±4.6(116)
1972	43.6(1568) YC = 1969	51.7±4.8(4113)	59.9±5.2(2264)	66.8±4.9(718)	71.8±4.8(419)	75.4±4.0(291)	79.0±4.5(264)
1973	42.5(1116) YC = 1970	51.8±4.8(5090)	59.0±5.5(1500)	66.2±5.1(995)	71.5±5.0(380)	75.6±5.1(289)	78.0±5.2(220)
1974	42.1(1737) YC = 1971	49.5±4.9(3648)	59.0±5.7(1559)	65.5±6.0(482)	71.4±5.4(374)	76.3±4.7(163)	79.2±5.8(109)
1975	42.4(885) YC = 1972	49.4±4.7(2832)	56.1±6.4(619)	65.5±6.3(342)	70.6±6.1(121)	75.2±4.8(101)	78.0±4.5(51)
1976	42.8(1269) YC = 1973	49.8±4.4(3008)	56.4±5.5(1477)	63.0±6.6(408)	70.4±5.5(251)	74.4±4.9(116)	78.4±4.6(90)
1977	42.6(1067) YC = 1974	50.1±4.3(1901)	56.4±5.5(456)	63.6±6.0(221)	68.8±5.8(81)	73.9±6.5(43)	
1978	42.2(1307) YC = 1975	49.6±4.4(1603)	56.4±5.1(420)	63.4±6.1(125)	69.9±5.5(56)		

[a] Sample sizes in parentheses; year classes (YC) follow diagonals.
[b] Lengths biased high for age group 3 (see text).

TABLE 2. Mean Fork Lengths (cm) ± SD for Female Striped Bass Tagged During Spring in the Sacramento-San Joaquin Estuary.[a]

Year		Age				
	4	5	6	7	8	9
1969	54.2±6.2(716)	63.6±5.3(1674)	70.2±5.5(1400)	75.8±6.1(573)	81.0±6.4(352)	85.8±6.5(277)
	YC = 1965	YC = 1964	YC = 1963	YC = 1962	YC = 1961	YC = 1960
1970	55.3±4.9(323)	64.2±4.9(821)	69.3±5.2(485)	75.2±5.4(329)	80.2±5.6(142)	84.2±5.2(80)
	YC = 1966					
1971	55.9±5.7(571)	63.9±5.3(658)	70.8±5.1(380)	76.6±5.5(204)	79.8±5.4(121)	83.2±4.5(51)
	YC = 1967					
1972	56.0±7.3(649)	65.5±4.6(2686)	72.6±5.0(841)	78.3±4.8(464)	82.2±4.5(221)	85.0±5.1(175)
	YC = 1968					
1973	55.3±6.0(593)	65.2±5.0(1303)	72.2±4.5(1416)	78.0±4.7(363)	82.5±5.2(162)	85.8±5.7(138)
	YC = 1969					
1974	52.4±6.2(508)	64.6±5.1(1602)	71.7±5.4(680)	78.0±5.1(495)	83.0±5.1(143)	86.7±6.1(92)
	YC = 1970					
1975	51.5±5.6(461)	62.7±6.2(597)	72.1±4.9(718)	77.0±5.2(195)	81.7±5.4(146)	85.2±5.3(51)
	YC = 1971					
1976	51.3±5.2(387)	62.7±5.4(1058)	70.0±5.9(449)	77.4±4.6(349)	82.2±5.2(107)	86.8±5.5(62)
	YC = 1972					
1977	52.9±5.4(190)	62.3±5.1(348)	70.3±4.7(237)	76.2±5.9(86)	82.2±5.5(47)	
	YC = 1973					
1978	54.1±4.7(141)	62.5±5.5(229)	69.8±5.3(138)	75.5±6.0(59)		
	YC = 1974					

[a] Sample sizes in parentheses; year classes (YC) follow diagonals.

TABLE 3.   Growth Rate Estimates for Young-of-the-Year Striped Bass in the Sacramento-San
Joaquin Estuary.[a]

Year class	Estimated date that bass reach 25.4 mm	Date	Mean fork length (mm)	Growth increment (mm)	Growth rate (mm/day)
1967	7/28	10/20	82.9	57.5	0.68
1968	7/7	10/11	87.8	62.4	0.64
1969	7/25	10/22	84.9	59.5	0.66
1970	7/1	10/18	88.2	62.8	0.58
1971	7/23	10/13	79.1	53.7	0.58
1972	7/6	10/17	82.7	57.3	0.55
1973	7/26	10/16	80.2	54.8	0.49
1974	—	—	—	—	—
1975	7/9	10/16	74.2	48.8	0.49

[a] Growth rates based on observed length of young bass captured in annual summer and fall tow net surveys
(Chadwick, Stevens, and Miller 1977; Miller unpubl. data).

Annual growth increments were calculated for each age group 3 to 8 from
spring data (i.e., 1974 growth increment for 4-yr-olds = age 5 $\overline{FL}$ in 1975 − age
4 $\overline{FL}$ in 1974). Observed mean lengths for 3-yr-old bass were biased high since
in spring about half the 3-yr-old population were shorter than the 38 cm FL
minimum tagging length. Therefore, growth increment estimates for age 3 bass
are biased low, but still are useful as an annual index of growth. Lengths for age
3 females were assumed to equal lengths observed for age 3 males because few
age 3 females were captured. They do not undertake a spawning migration until
they are 4 or 5-yr-old (Chadwick 1967). Back calculated lengths demonstrate
that male and female striped bass are essentially the same length up to age 3
(Scofield 1931, Robinson 1960).

I examined fluctuations in the annual growth increments for evidence that
they may have resulted from variations in forage availability or intraspecific
competition. For this analysis, the mean of the annual growth increments for ages
3 to 8 were calculated for each year for each sex; the average for male and
female bass was then used as an estimate of the annual mean growth of adult
striped bass. Abundance estimates for two important forage species, northern
anchovy, *Engraulis mordax,* and shiner perch, *Cymatogaster aggregata* (Thomas
1967) were available from midwater trawl surveys during August, September,
and October from 1969 to 1973. Two measures of adult bass abundance were
used to examine intraspecific effects. One abundance index was calculated
from commercial passenger fishing boat catches (Stevens 1977b); the other
abundance index consists of Petersen population estimates (Stevens 1977a).

RESULTS
Von Bertalanffy Growth Equation
Growth of adult striped bass collected from 1969–1976 in the Sacramento-San
Joaquin Estuary was described well by the von Bertalanffy growth equation
(Figure 2). Correlation coefficients (r) between observed and predicted lengths
from the von Bertalanffy equation were 0.998 for males and 0.996 for females.
Male bass grew from about 40 cm at age 3 to about 86 cm at age 12; while female
bass grew from about 40 cm at age 3 to about 96 cm at age 12. Hence, females
grew more rapidly than males and by age 6 ($\overline{FL}$ = 70.7 cm) were as large as
7-yr-old males ($\overline{FL}$ = 70.6 cm).
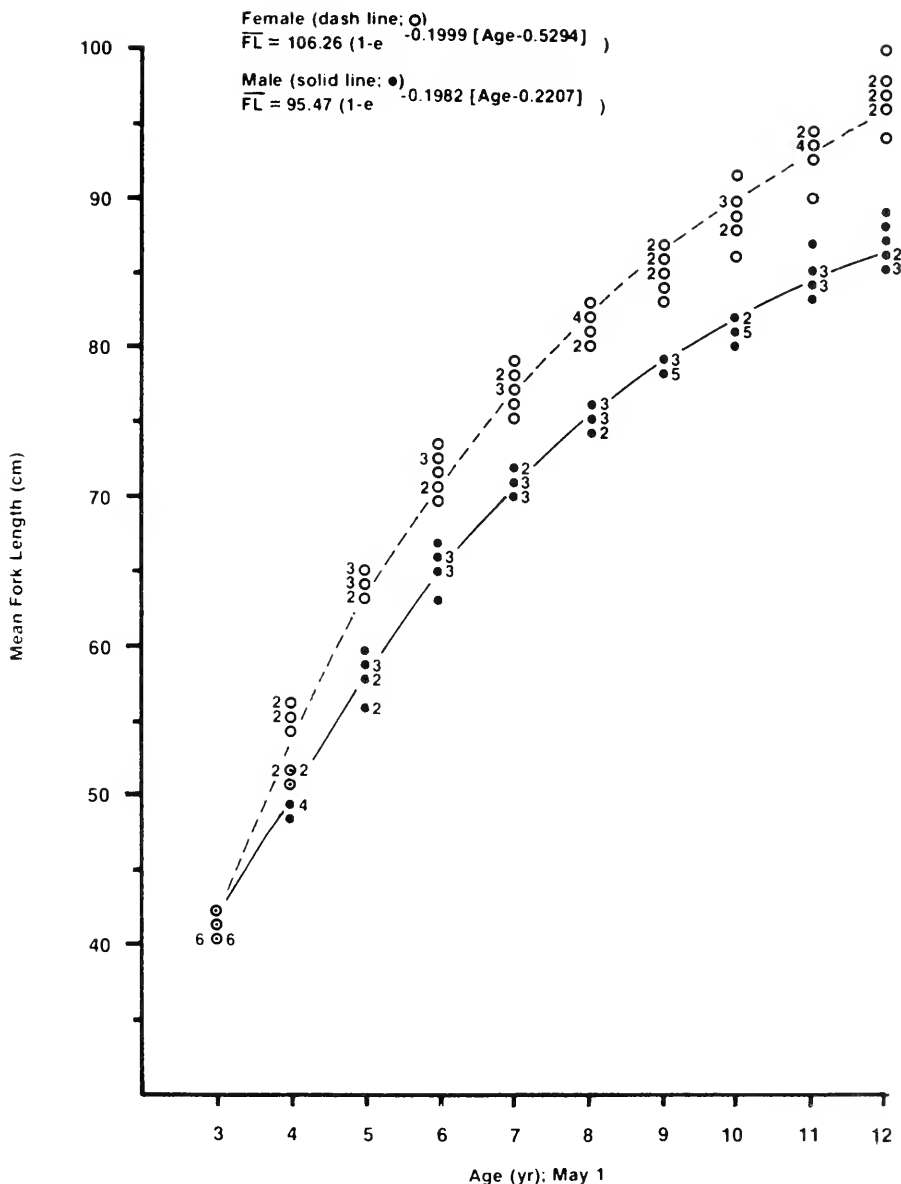
FIGURE 2. Von Bertalanffy growth curves for striped bass sampled during spring (1969–1976) in the Sacramento-San Joaquin Estuary. Equations were calculated from annual mean lengths. Numbers next to data points indicate number of overlapping points.

Seasonal Growth

Growth varied seasonally. Length increased from May to November and then, except for 3 to 5-yr-old females, showed little or no increase until the following May (Table 4). Three to 5-yr-old females had a mean length increase of 2.3 cm from November to May which is about 0.46 cm/month and about one-third as

fast as the summer-fall growth rate (1.46 cm/month) for these fish. No data were available to determine if 3 to 5-yr-old females grew constantly throughout winter at this low rate. An inconsistency is that among age 4 to 8 males and 7 to 8 females the mean fork length in November is larger than the mean fork length for the next age group the following May.

TABLE 4. Seasonal Growth of Striped Bass (1969–1977) in the Sacramento-San Joaquin Estuary. Lengths are Monthly Grand Means; Growth Rates (cm/month) are Given as Regression Coefficients (b) ± Standard Errors (SE).

	Age					
Males	3	4	5	6	7	8
May	40.2 *	50.5	58.0	65.0	70.6	75.1
June	43.5	53.7	61.9	68.4	74.7	77.9
July	44.5	53.9	63.4	69.9	74.8	79.2
Aug.	47.0	56.7	64.5	70.1	75.1	78.6
Sept	49.1	58.0	64.7	70.1	75.1	79.1
Oct.	50.3	58.4	65.2	70.8	75.6	79.1
Nov	50.5	58.7	65.5	72.6	76.3	79.9
b	1.75	1.36	1.09	0.99	0.69	0.66
SE	0.17	0.19	0.25	0.21	0.23	0.19
Females						
May	40.2 *	53.9	63.8	72.1	77.0	81.6
June	43.8	54.7	64.0	73.3	78.2	82.0
July	45.1	56.2	66.9	74.2	79.6	84.2
Aug.	47.0	59.2	68.4	74.9	80.4	84.6
Sept	49.8	60.5	68.6	75.2	80.4	84.9
Oct.	50.9	61.0	69.4	75.5	81.3	85.6
Nov	51.3	61.4	70.1	77.1	82.1	85.8
b	1.86	1.41	1.12	0.73	0.80	0.67
SE	0.17	0.16	0.15	0.07	0.08	0.09

* Average of the modal fork lengths for males captured in fyke traps (1969–1976).

Annual Size Variations

Significant differences (P < 0.001) among spring mean lengths of striped bass (sexes combined) at the same age were found for age groups 4 to 7. *A posteriori* comparisons demonstrated that the 1970 and latter year classes were significantly smaller (P < 0.01) at all ages than the 1965–1969 year classes, which averaged 2 cm larger over this age range (Tables 1 and 2). However, growth rates over this age range (Figure 3) for the 1965–1969 year classes (7.7 cm/month) were not significantly different from the 1970 and latter year classes (7.4 cm/month).

Reduced first year growth (Table 3) apparently contributed to the reductions in lengths observed for the post-1969 year classes. The average growth rate for the 1970–1975 year classes as young-of-the-year was 0.54 mm/day, 18% lower than the average growth rate estimate of 0.66 mm/day for the 1967–1969 year classes as young-of-the-year. Except for age 4, mean lengths of adults (sexes combined) in spring were significantly correlated with growth rates estimated for the same year classes as young-of-the-year (Table 5). The correlation coefficients tended to increase with age because at ages ≥ 4 the 1975 year class dropped from the analysis and at age 6 the 1973 year class was eliminated. Dropping these year classes improved the correlation coefficients because as adults their lengths were greater than expected from the relation between young growth and adult size for the other year classes.
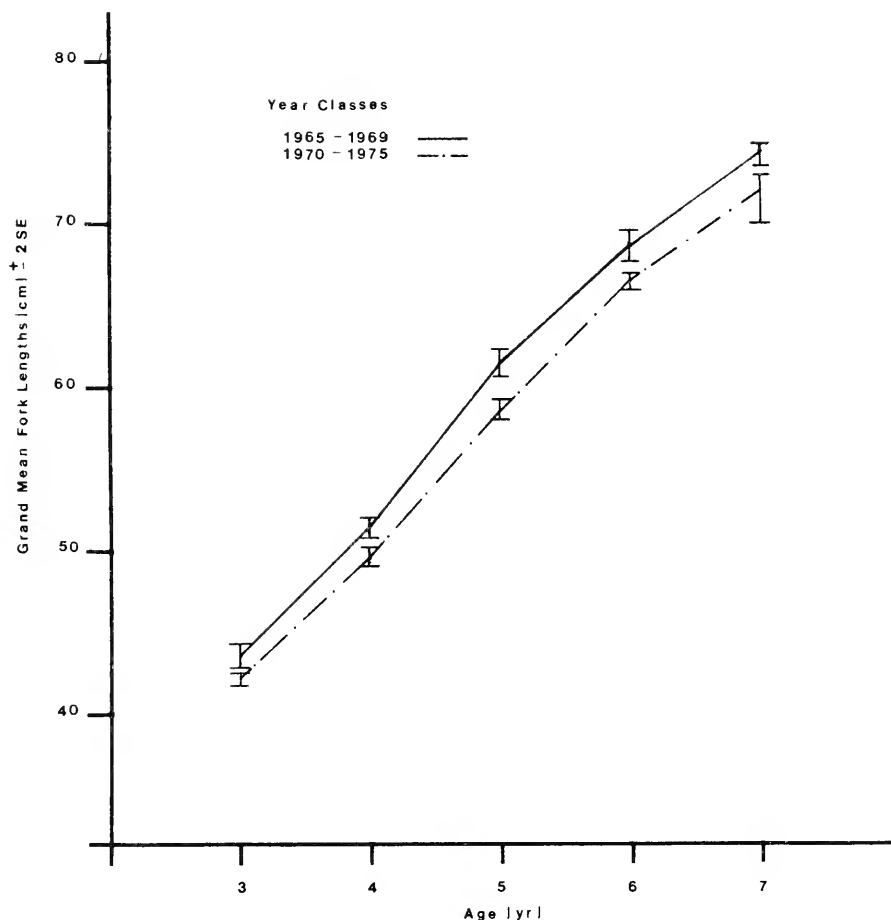
FIGURE 3.   Growth of striped bass sampled during spring in the Sacramento-San Joaquin Estuary
from the 1965–1969 and 1970–1975 year classes. Sexes combined.

TABLE 5.   **Growth Rates of Young-of-the-Year Striped Bass (July–October) and Mean
Lengths, Sexes Combined, Attained in Spring During Subsequent Years of Adult
Life (r = Correlation Coefficient).**

	Young bass growth rate (mm/day)	Spring fork length (cm)				
Year class		Age 3 $R=0.76^*$	Age 4 $r=0.72$	Age 5 $r=0.93^{**}$	Age 6 $r=0.97^{**}$	Age 7 $r=0.95^*$
1967	0.68	44.5	51.3	63.0	69.7	75.1
1968	0.64	43.1	52.2	61.9	69.2	74.5
1969	0.66	43.6	52.2	61.8	70.0	74.5
1970	0.58	42.5	49.8	59.3	66.6	72.6
1971	0.58	42.1	49.7	59.0	67.0	71.5
1972	0.55	42.4	50.0	58.9	66.5	
1973	0.49	42.8	50.3	58.5		
1974		42.6	49.9			
1975	0.49	42.2				

* = P < 0.05
** = P < 0.01

The mean of the annual growth increments from 1969 to 1977 for male bass decreased from 7.3 cm for 4-yr-olds to 3.0 cm for 8-yr-olds (Table 6), while the mean annual growth increment for females over the same ages decreased from 9.9 cm to 3.8 cm. The mean of the annual growth increments during a given year for ages 3 to 8 (annual mean growth) varied from 5.2 cm to 7.2 cm for males and 6.4 cm to 8.2 cm for females. However, variations in annual mean growth from 1969 to 1977 were significantly correlated for males and females ($r = 0.90$; $P < 0.01$).

TABLE 6. Annual Growth Increments (cm) of Striped Bass in the Sacramento-San Joaquin Estuary.

| | Males | | | | | | | | | |
| | Year | | | | | | | | | |
Age	1969	1970	1971	1972	1973	1974	1975	1976	1977	Mean
3*	7.2	6.0	8.6	8.2	7.0	7.3	7.4	7.3	7.0	7.3
4	8.2	7.5	9.4	7.3	7.2	6.6	7.0	6.6	6.3	7.3
5	6.4	6.5	8.5	6.3	6.5	6.5	6.9	7.2	7.0	6.9
6	5.3	5.8	6.6	4.7	5.2	5.1	4.9	5.8	6.3	5.5
7	4.4	4.1	5.0	3.8	4.8	3.8	3.8	3.5	(4.2)+	4.2
8	2.7	2.6	4.8	2.6	3.6	1.7	3.2	(3.0)+	(3.0)+	3.0
Annual mean	5.7	5.4	7.2	5.5	5.7	5.2	5.5	5.6	5.6	5.7
Age	Females									Mean
3*	11.7	11.4	12.9	11.7	9.9	9.4	8.9	10.1	11.5	10.8
4	10.0	8.6	9.6	9.2	9.3	10.3	11.2	11.0	9.6	9.9
5	5.7	6.6	8.7	6.7	6.5	7.5	7.3	7.6	7.5	7.1
6	5.0	7.3	7.5	5.4	5.8	5.3	5.3	6.2	5.2	5.9
7	4.4	4.6	5.6	4.2	5.0	3.7	5.2	4.8	(4.7)+	4.7
8	3.2	3.0	5.2	3.6	4.2	2.2	5.1	(3.8)+	(3.8)+	3.8
Annual mean	6.7	6.9	8.2	6.8	6.8	6.4	7.2	7.2	7.0	7.0

* Biased low (see text).
+ Growth increment not available for this year; therefore, the mean increment for the age group was used in calculating the annual mean increment for this year.

For all ages, except age 4 females, the largest annual growth increments occurred from spring 1971 to spring 1972 (Table 6). That year estimated average annual mean growth for sexes combined exceeded the average for all other years by 1.5 cm.

Effects of Forage Abundance and Intraspecific Competition

The higher average annual mean growth in 1971 corresponded to the largest forage abundance indices observed for anchovies and shiner perch in San Francisco and San Pablo bays (Figure 4). The 1971 abundance indices for anchovies and shiner perch were 48% and 38% greater, respectively, than the mean abundance indices for 1969, 1970, 1972, and 1973, during which essentially no variation was observed in annual mean growth for striped bass.

There was no obvious relationship between bass growth and either Stevens' (1977b) striped bass abundance indices or Petersen population estimates (Bailey 1951) for adult bass (Figure 4). While peak growth occurred when abun-

dance was moderately low, growth increments coinciding with lower abundance measurements were equivalent to growth increments measured at some of the highest abundance estimates.
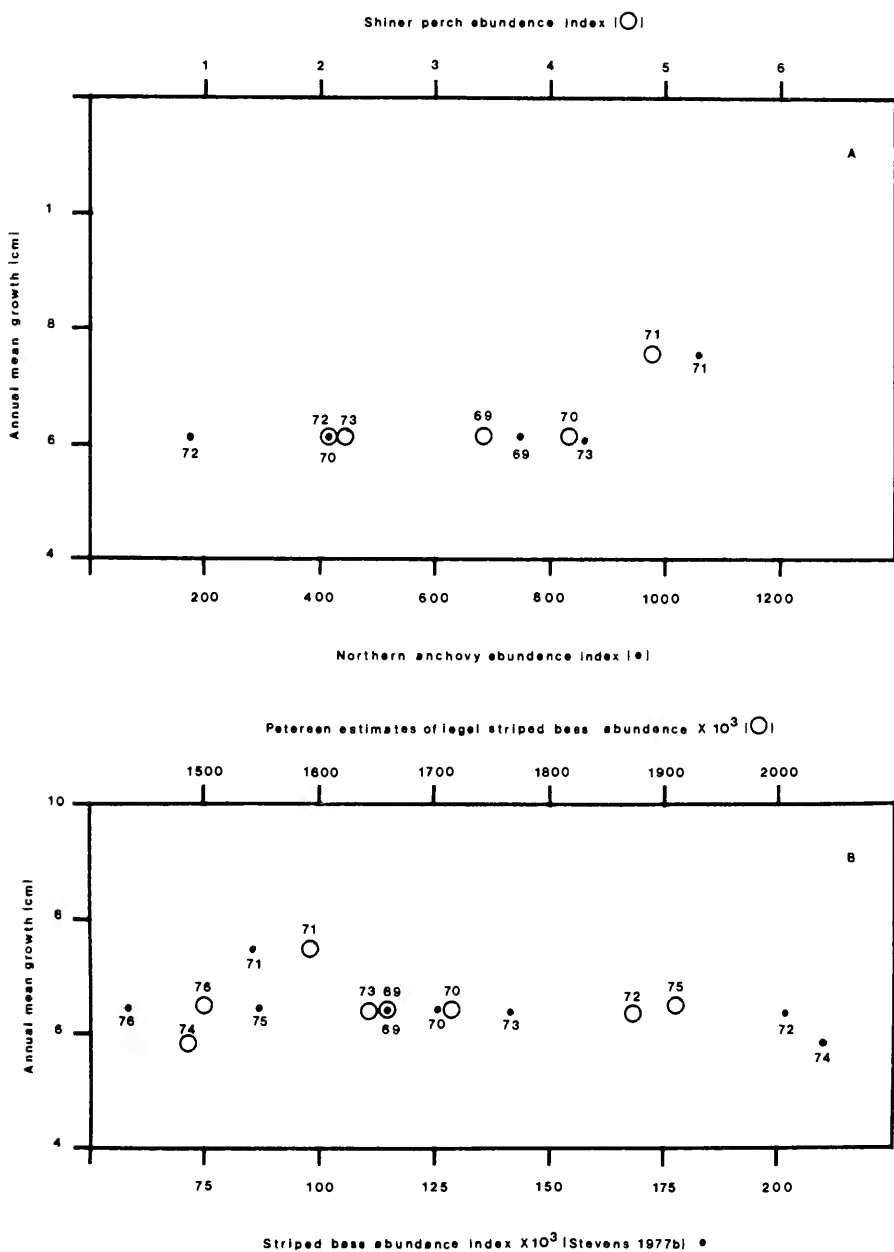

FIGURE 4.   Adult striped bass annual mean growth vs. forage abundance estimates in San Francisco and San Pablo bays and adult striped bass abundance estimates.

DISCUSSION

The von Bertalanffy growth equation described the general form of adult striped bass growth well but underestimates maximum length. Asymptotic lengths predicted by the equation were 95.5 cm for males and 106.3 cm for females. Mean lengths of the largest bass observed each spring were 101.1 cm for males and 113.4 cm for females. This underestimation probably resulted from restricting the analysis to ages 3 to 12.

Growth occurred primarily between May and November. Comparisons of lengths for various age groups in November with the next older age group in May suggested some winter growth occurred among 3 to 5-yr-old females. In contrast 4 to 7-yr-old male bass lengths in May were consistently smaller than lengths in the previous November. A similar discrepancy was also observed for females at age 6 (fall) and 7 (spring). These discrepancies apparently reflect unresolved sampling biases.

The 1970 and later year classes averaged about 2 cm smaller than the 1965–69 year classes at all ages; however, growth rates from ages 3 to 7 did not significantly differ between these two groups. The size reduction was associated with decreased growth of the same year classes as young-of-the-year which may have been due to reduced food abundance. From 1968 to 1975 young-of-the-year bass growth was significantly correlated ($r = 0.81$, $P < 0.05$) with indices of abundance (J. Orsi, Assoc. Fish. Biol., Calif. Dept. Fish and Game, pers. commun.) of their major food organism, *Neomysis mercedis*. Survival of young bass also has decreased since 1970 due to State and Federal water projects increasing diversions from the striped bass nursery and reducing freshwater flows which disperse young bass through the estuary (Chadwick, Stevens, and Miller 1977). Abundance of *Neomysis* may have been reduced by the same water diversions (Orsi and Knutson 1979). Thus, the water projects may be reducing both survival and growth of striped bass.

Other studies also have demonstrated that size differentials established in young fish are maintained throughout life. Merriman (1941) reported that 2 and 3-yr-old striped bass of the dominant 1934 year class sampled in Connecticut grew at about the same rate but averaged at least 2 cm smaller than members of the 1933 and 1935 year classes at age 3. Therefore, the observed size difference developed early in life. Also, Tiller (1943) reported that larger striped bass yearlings in Chesapeake Bay maintained their size advantage in subsequent years.

Mean lengths of 4 to 7-yr-old striped bass in 1957–58 (Robinson 1960) averaged about 5.6 cm longer than in 1925–28 (Scofield 1931). Robinson suggested this size increase might be a response to decreased intraspecific competition resulting from a decline in striped bass abundance. Appropriate data are not available for the 1920's, but a general decline in fishing success suggests bass abundance declined from the late 1930's to the time of Robinson's study in the mid-1950's (Chadwick 1962). Similarly, McGie and Mullen (1979) reported that growth increments of striped bass in Umpqua River, Oregon, were larger during the early 1940's when the striped bass population was smaller (as indicated by the commercial catch statistics) than the 1954–68 period.

Increases in the size of adult striped bass have also been observed since 1957–58 but were smaller than observed between Scofield's and Robinson's studies.

The average length of ages 4 to 7 increased 1.8 cm from 1957–58 to 1961–65 (Miller and Orsi 1969), and 1.2 cm from 1961–65 to 1969–78. The size increase from 1961–65 to 1969–78 is consistent with the intraspecific competition hypothesis as average adult abundance probably was lower from 1969 to 1978 (Stevens 1977*b*). However, the size increase from 1957–58 to 1961–65 is not consistent with this hypothesis, since bass probably were more abundant from 1961 to 1965 (Stevens 1977*b*). Therefore, other factors apparently also affected these results. The differences observed in the size of the bass since Robinson's study have been within the size range I have attributed to differences in first year growth rates, therefore may have resulted from differences in growth of immature fish.

Robinson (1960) observed fluctuations in annual growth from 1952 to 1956 but did not have sufficient data to explain them. Very little variation occurred among the mean annual growth increments during my study except for 1971 when a substantial increase in growth was observed for almost all ages. This corresponded with the largest forage abundance index observed between 1969 and 1973. I also examined potential effects of intraspecific competition. Although bass abundance did not fluctuate much during my study, the abundance estimate was moderately low in 1971 when the highest growth was observed. However, growth was essentially equal at lower and higher population abundance levels. Possibly the high growth rate in 1971 resulted from the combination of high forage abundance and moderately low bass abundance.

Although growth (Miller and Orsi 1969) and abundance (Stevens 1977*b*) data also are available from 1961 to 1965, I did not use them to analyze effects of intraspecific competition on growth because some of the growth data did not appear reliable. For example the growth increment for age 3 females was unrealistically low in 1963 (3.3 cm) and the increment for age 4 females was unrealistically high in 1964 (15 cm). To resolve specifically how changes in forage abundance and intraspecific competition affect adult striped bass growth more observations are needed.

ACKNOWLEDGMENTS

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DIFFERENTIAL EFFECTS OF LIVESTOCK USE ON HABITAT STRUCTURE AND RODENT POPULATIONS IN GREAT BASIN COMMUNITIES [1]

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Effects of livestock grazing on habitat structure, measured in terms of relative composition of plant life forms (trees, shrubs, forbs, graminoids), were assessed for 26 Great Basin habitat types in northeastern California and northwestern Nevada. Livestock grazing impact was quantified by comparison of "present" plant life form composition of each habitat type (determined by sampling 132 stands of vegetation) with estimates of "potential" plant life form composition based on U.S. Soil Conservation Service range site descriptions and other synecologic literature. Rodent populations were censused in livestock-grazed and -ungrazed communities of seven representative habitat types. Livestock grazing resulted in decreased relative abundance of herbaceous vegetation, particularly perennial bunchgrasses, in the study area. This had the effect of decreasing diversity of plant life forms in the more xeric habitats and increasing diversity of plant life forms in the more mesic habitats. Microtine rodents were consistently found in lower abundance in livestock-grazed than -ungrazed communities. Other species (*Eutamias minimus, Perognathus parvus,* and *Peromyscus maniculatus*) appeared to act as "decreasers" in xeric habitats and "increasers" in mesic habitats. Percentage change (from "potential" to "present" conditions) in rodent community diversity was positively correlated with percentage change in plant life form diversity. Change in plant life form diversity accounted for 79% of the variation in change in rodent species diversity.

INTRODUCTION

The quality of habitat for animals is strongly dependent upon habitat structural features. Organisms are more able to partition their exploitation of resources in structurally complex than structurally simple environments, and animal species diversity has often been related to habitat structural diversity (Pimlott 1969, Pianka 1973, Balda 1975). Habitat diversity can be measured in many ways; species diversity and foliage cover diversity are two of the most common. Plant life forms (i.e., trees, shrubs, graminoids, forbs) also are important components of habitat structure (Bossenbroek *et al.* 1977) and some recent attempts to provide land management guidelines for habitat improvement have emphasized their importance to vertebrate fauna (Thomas *et al.* 1976).

Livestock grazing on rangelands exerts a controlling influence on plant community structure, primarily as a result of selective defoliation of forage species (Stoddart, Smith, and Box 1975). Grazing by domestic cattle and sheep has

resulted in alteration of plant communities in many areas of western North America during the past century. This has been particularly true in the Great Basin region of the United States (U.S. Bureau of Land Management 1974; Box, Dwyer, and Wagner 1976.)

The nature of livestock grazing influence, however, varies with different types of biotic communities. An understanding of the differential effects of livestock impact on plant communities is, therefore, of value in interpreting livestock effects on native animal communities. It was the purpose of the present study to investigate the impact of livestock grazing on habitat structure, measured in terms of plant life forms, in a variety of Great Basin communities and to examine the implications of habitat change for rodent populations. Rodents are important components of consumer trophic levels and are potential prey for numerous carnivorous mammals, birds, and reptiles, as well as parasites and microorganisms. Rodent communities are relatively easily censused, and the typically small home range size of these animals minimizes problems associated with unraveling the confounding effects of juxtaposition of habitat patches on animal community structure.

Study Area

The study area was approximately 250,000 ha of rangeland located in and around Surprise Valley and the Warner Mountains, northeastern California and northwestern Nevada, near Cedarville, California. The area was stratified by habitat type, and 26 habitat types, ranging from shadscale-dominated, *Atriplex confertifolia,* to white fir, *Abies concolor,* communities (Table 1), were studied. A *habitat type (sensu* Daubenmire 1952) is all the area (sum of discrete units) that now supports—or within recent time has supported, and presumably is still capable of supporting—one plant association recognizable by a distinct assemblage of species and productivity. Thus, a given habitat type includes all land areas *potentially* capable of producing similar plant communities.

Elevation ranged from 1350 m in the lowest part of Surprise Valley to 3000 m at the crest of the Warner Mountains. Total annual precipitation averaged from 150 mm in the lowest areas to 500 mm in the Warner Mountains (Summerfield and Bagley 1974). The majority of the land area was characteristic of the Great Basin desert biome. Dominant plant species included shadscale, greasewood, *Sarcobatus vermiculatus;* low sagebrush, *Artemisia arbuscula,* big sagebrush, *A. tridentata;* silver sagebrush, *A. cana;* rabbitbrush, *Chrysothamnus* spp.; bitterbrush, *Purshia tridentata;* snowberry *Symphoricarpos albus;* western juniper, *Juniperus occidentalis;* curlleaf mountain mahogany, *Cercocarpus ledifolius;* yellow willow, *Salix lutea;* quaking aspen, *Populus tremuloides;* white fir; Nevada bluegrass, *Poa nevadensis;* Sandberg bluegrass, *P. secunda;* sedges, *Carex* spp.; baltic rush, *Juncus balticus;* Great Basin wildrye, *Elymus cinereus;* Idaho fescue *Festuca idahoensis;* bluebunch wheatgrass, *Agropyron spicatum;* Thurber needlegrass, *Stipa thurberiana;* squirreltail, *Sitanion hystrix;* Indian ricegrass, *Oryzopsis hymenoides;* and desert saltgrass, *Distichlis stricta.* The vegetation, soils, and general nature of the study area have been described by Summerfield and Bagley (1974).

The principal livestock use has been by cattle; there has been minor use by sheep and feral horses in recent years. Livestock utilized the study area between

TABLE 1. Vegetation Zones, Association Groups, and Habitat Types of the Study Area. These have been arranged tentatively along a soil moisture gradient, first by zones, then by association groups, and then by habitat type.

	Zones	Association groups	Habitat types
Xeric ↑	big sage/bluebunch wheatgrass	shadscale	shadscale/Indian ricegrass shadscale-big sage
		greasewood	greasewood/Great Basin wildrye greasewood/saltgrass
		low sagebrush	low sage/bluegrass-squirreltail low sage/Idaho fescue-Sandberg bluegrass low sage-rabbitbrush low sage/Idaho fescue
		big sagebrush	big sage/Indian ricegrass big sage/squirreltail-Indian ricegrass big sage/Great Basin wildrye low sage/bluebunch wheatgrass low sage/bluebunch wheatgrass-Great Basin wildrye big sage/bluebunch wheatgrass-Thurber needlegrass
		bitterbrush-big sage/bluebunch wheatgrass juniper/big sage/bluebunch wheatgrass big sage/Idaho fescue big sage-snowberry/Idaho fescue	big sage-silver sage/Great Basin wildrye
		curlleaf mountain mahogany	curlleaf mountain mahogany/big sage/Idaho fescue
		silver sagebrush	silver sage/Nevada bluegrass
		baltic rush	baltic rush
		apsen	aspen
		Nevada bluegrass	willow/Nevada bluegrass Nevada bluegrass-sedge
Mesic ↓	white fir	white fir	white fir

April and October each year at an average annual stocking rate of approximately 0.16 AUM (animal unit month—one adult cow with one calf for one month) per ha between 1972 and 1976; most of the shrub-dominated rangeland was in "fair" range condition with a "stable" trend in 1976 (U.S. Bureau of Land Management 1979). Greatest effects of overgrazing by sheep and cattle in this area are believed to have occurred during the late 19th and early 20th centuries (U.S. Bureau of Land Management, Susanville District Office, unpubl. manuscript).

METHODS

Vegetation

Livestock grazing effects on habitat structure, measured in terms of changes in relative proportions of vascular plant life forms (trees, shrubs, graminoids, forbs), were quantified by comparison of measured "present" vegetation parameters with descriptions of the "potential" natural vegetation stratified by habitat type. The data were collected as part of a larger effort to obtain baseline data for livestock grazing management analysis.

During the summer of 1976, 132 stands of vegetation were sampled to determine species composition and canopy coverage of the 26 habitat types. Canopy coverage was defined as the percentage of the ground included in a vertical projection of the total natural spread of foliage of the individuals of a species; dead portions of the canopy were not included. The sampling was stratified by habitat type on the basis of soil type maps (Summerfield and Bagley 1974). The number of stands sampled per habitat type varied with our subjective appraisal of the relative importance (amount of area occupied and potential productivity) and heterogeneity of the present vegetation of each habitat type. Canopy coverage of herbaceous species was determined using a quadrat estimation technique (Daubermire 1959) with 30 0.1-m^2 (20 x 50 cm) quadrats systematically placed at 1.5-m intervals along two parallel 25-m transect lines in each stand. In tree-dominated (white fir, aspen, curlleaf mountain mahogany) communities, canopy coverage of all species was determined in this manner. Canopy coverage of woody perennials in the shrub-grass communities was determined using the line-interception technique (Canfield 1941) and 25-m transect lines placed parallel to each other and systematically spaced at 5-m intervals. The number of transect lines used per stand varied as a function of vegetation heterogeneity and was determined on the basis of a mean-cover-sample-size curve (Hanley 1978) constructed in the field for each stand as it was being sampled. Shrub and tree canopy coverage in meadow and riparian communities was measured on low-level infrared aerial photographs taken according to procedures described by Meyer (1973).

Descriptions of the potential natural vegetation of the meadow and shrub-grass habitat types were provided by Soil Conservation Service range site descriptions (U. S. Soil Conservation Service 1965). These represented the best estimates of species composition and percentage of total net primary productivity contributed by each species in each habitat type in the absence of "unnatural disturbance" (see U. S. Soil Conservation Service 1976). They were based on evaluation of relict vegetation and associated soils in areas that have been

subjected to minimal "abnormal" disturbances, evaluation of similar areas currently disturbed in varying degrees, and relevant historical accounts and botanical literature of the area (U. S. Soil Conservation Service 1976). These descriptions had been prepared only for habitat types meeting the Soil Conservation Service's definition of "rangeland", however, and tree-dominated communities were not included. Synecologic descriptions of aspen (Houston 1954, Hutchins 1965, Beetle 1974), white fir (Franklin and Dyrness 1973), and curlleaf mountain mahogany (Dealy 1975) habitat types provided similar descriptions of the potential natural vegetation of these habitat types.

Mean canopy coverage was calculated for each species in each of the 132 stands sampled, and mean canopy coverage of each species in each habitat type was subsequently calculated. Total canopy coverages of trees (including willow), shrubs, graminoids, and forbs were calculated and expressed as proportions of the total coverage of all species for each habitat type. These data represent the average percentage composition of these four plant life forms in each habitat type when sampled in 1976. Similar proportional values were determined for the potential natural vegetation on the basis of the appropriate Soil Conservation Service range site descriptions or other synecologic data.

Livestock grazing effects on structural diversity of the habitat types (see Whittaker 1965, McIntosh 1967, Hutchinson 1958) were determined by comparing diversity indices of the present plant life form composition with corresponding potential values for each habitat type. The diversity index used was the Shannon index (Shannon and Weaver 1949), which is appropriate for samples of "indefinitely large" communities (Pielou 1975). It is defined as

$$H' = -\Sigma P_i \log P_i$$

where P_i is the proportion of the community belonging to the ith category. For four categories (trees, shrubs, graminoids, forbs) the maximum value of H' is 0.602. The minimum value is always zero (and occurs when all dominance is concentrated in only one category). The index is influenced by category richness (number of categories) and evenness of distribution among categories. A measure of evenness may be obtained by dividing the calculated H' by the maximum possible value of H' for the corresponding number of categories. This is expressed as H'/H'_{max}, and values range from greater than zero to a maximum of 1.000.

Rodent Communities

Livestock grazing effects on rodent communities were quantified by comparison of rodent species composition of seven pairs of "grazed" and "ungrazed" habitat types censused during the summer of 1977: Shadscale/Indian ricegrass, greasewood/Great Basin wildrye, low sage/Idaho fescue, big sage/bluebunch wheatgrass-Thurber needlegrass, big sage/Idaho fescue, aspen, and Nevada bluegrass-sedge habitat types. Vegetation parameters were not measured at the sites where rodents were censused. However, the "grazed" communities were selected as being representative of the average plant species composition and life form structure of the habitat types sampled in 1976. The "ungrazed" communities were relict areas (*sensu* Clements 1934) of the respective habitat types and were representative of the potential plant species composition and life form

structure described in the Soil Conservation Service range site descriptions and other synecologic data.

Populations were censused by a systematic placement (two parallel lines 15 m apart with traps located at 6-m intervals) of 224 snap traps (196 museum specials and 28 commercial rat traps) baited with moistened oatmeal, 50 Sherman live traps baited with dry oatmeal, and 50 1-gallon pitfall can traps in each community sampled. Trapping was conducted during 3 consecutive days and nights with all traps being checked and baited twice daily. Densities of rodents were not determined; rather, abundance indices (total number captured) were used. However, densities and catch indices are usually highly correlated (Hansson 1967, Petticrew and Sadlier 1970).

The Shannon index (H'), species richness (number of species), and evenness (H'/H'$_{max}$) were used as measures of rodent community diversity.

RESULTS AND DISCUSSION

Vegetation

Plant Life From Composition

The major difference between the present and potential structure of nearly all habitat types was a much reduced percentage composition of graminoids and a concomitant increased percentage composition of shrubs in the present vegetation (Table 2). Greatest differences occurred in the greasewood/saltgrass, big sage/Indian ricegrass, big sage/Great Basin wildrye, big sage/bluebunch wheatgrass, big sage-snowberry/Idaho fescue, and big sage-silver sage/Great Basin wildrye habitat types. The tall perennial bunchgrass dominants received the greatest adverse impact from livestock grazing. Cheatgrass, *Bromus tectorum*, and Sandberg bluegrass comprised most of the grass cover of these habitats when sampled in 1976.

TABLE 2. Percentage Composition of Plant Life Forms in Each Habitat Type at Potential and Present Conditions, Averaged by Association Groups (see Table 1).

Association group	Trees		Shrubs		Graminoids		Forbs		No. of stands sampled
	potential	present	potential	present	potential	present	potential	present	
Shadscale	0	0	82	99	15	1	3	0	9
Greasewood	0	0	41	91	56	4	3	5	7
Low sagebrush	1	1	42	52	36	33	21	14	18
Big sagebrush	4	3	29	65	56	28	11	4	54
Curlleaf mountain mahogany	46	76	9	8	36	15	9	1	6
Silver sagebrush	0	0	39	72	48	21	13	7	3
Baltic rush	0	0	0	8	70	43	30	49	4
Aspen	79	83	4	4	1	8	16	5	7
Nevada bluegrass	38	15	1	23	52	42	9	20	18
White fir	95	95	1	1	3	3	1	1	6

The aspen habitat type was heavily used by livestock. Increased percentage composition of graminoids in the present as compared to the potential conditions was due to a marked decreased percentage composition of forbs in the aspen understory. The lush vegetation of perennial forbs that characterize the potential understory was not present in the livestock-grazed aspen stands sam-

pled in 1976. Total forb canopy coverage averaged only 5.9%. Also of importance was the absence of successful aspen reproduction due to consumption of the root sprouts by livestock. This made for a very open understory lacking a midstratum of young aspen trees.

Increased percentage composition of shrubs was evident in the wet meadow and willow riparian habitat types (Nevada bluegrass-sedge and willow/Nevada bluegrass habitat types, respectively). Percentage composition of trees (willow) in the willow/Nevada bluegrass habitat type decreased by approximately 60%, thus increasing the percentage composition of the other plant life forms. Another important difference between livestock-grazed and -ungrazed meadows was the 30–50 cm deep herbaceous layer of protected meadows versus the closely "mowed" surface of the grazed meadows.

The white fir habitat type did not show any appreciable effects of livestock use, presumably due to the reluctance of livestock to use these communities, except along their edges. The white fir overstory was very dense and the understory sparse. Total cover of nonconifer vascular understory averaged only 4.7%.

Plant Life Form Diversity

Livestock grazing-induced changes in the percentage composition of plant life forms caused a reduction in structural diversity in 65% of the habitat types (Table 3). The reductions were most pronounced in the drier habitats, such as the shadscale/Indian ricegrass, shadscale-big sage, greasewood/saltgrass, and big sage/Indian ricegrass habitat types, where shrubs presently dominated the communities to (or nearly to) the exclusion of herbaceous species. These were habitats where shrubs dominate the potential vegetation as well. Any reduction of herbs, with corresponding increased relative dominance of shrubs, tended to decrease the structural diversity within such habitats (Table 3).

TABLE 3. Average Diversity (H') of Plant Life Forms in Habitat Types at Potential and Present Conditions and Average Percentage Change from Potential to Present. Habitat types have been grouped by their potential dominant life form.

Potential dominant life form	Number of Average diversity at potential	Average diversity at present	Average percent increase (+) or decrease (−)	Number of habitat types with increased diversity	Number of habitat types with decreased diversity
Tree [1]	0.295	0.321	+14.9	1	2
Shrub	0.360	0.189	−52.3	1	7
Graminoid	0.368	0.371	+11.5	6	8
Forb	–	–	–	0	0

[1] Four habitat types were potentially dominated by trees. The last two columns sum to 3, because there was no change in diversity in the white fir habitat type.

On the other hand, reduced percentage composition of herbaceous species with concomitant increased percentage composition of shrubs, in herb-dominated communities (such as the Nevada bluegrass-sedge and baltic rush habitat types), tended to increase the structural diversity within these communities. Increased structural diversity within the low sage-rabbitbrush habitat type resulted from invasion by juniper trees; and diversity within the bitterbrush-big sage/bluebunch wheatgrass habitat type increased as a result of both increased per-

centage composition of juniper and decreased composition of grass. Plant life form diversity increased within the willow/Nevada bluegrass habitat type due to a reduction in the dominance of willows and an increased abundance of shrubs.

Rodents

A total of 221 rodents was captured in the seven livestock-grazed communities as opposed to 302 captured in the ungrazed communities (Table 4), thus indicating a reduction in rodent density due to livestock grazing in those seven habitat types. However, responses varied greatly among rodent species and habitat types. Rodent community diversity also responded differentially to livestock grazing, decreasing in some habitat types and increasing in others.

Differential Response by Species

Species dependent upon perennial herbs for food and cover were consistently less abundant (or absent) in livestock-grazed than -ungrazed communities. These included the little pocket mouse, *Perognathus longimembris*; desert wood rat, *Neotoma ledpia*; all three microtine rodents (the montane vole, *Microtus montanus,* the long-tailed vole, *Microtus longicaudus,* and the sagebrush vole, *Lagurus curtatus*); and western jumping mouse, *Zapus princeps*. The little pocket mouse and desert wood rat were closely associated with Great Basin wildrye in the ungrazed greasewood/Great Basin wildrye community. The microtine rodents and western jumping mouse are dependent on dense herbage for both food and cover (Larrison 1976). It is probable that these species are consistent "decreasers" under livestock grazing pressure due to their strong dependence on herbaceous vegetation, particularly perennial grasses.

Three granivorous species, however, demonstrated differential responses to livestock grazing. These were the least chipmunk, *Eutamias minimus*; Great Basin pocket mouse, *Perognathus parvus*; and deer mouse, *Peromyscus maniculatus.* The least chipmunk and deer mouse were present in all of the seven habitat types; the Great Basin pocket mouse was present in all but two. These three widely occurring species exhibited similar responses to livestock grazing—they responded as "decreasers" in the driest habitat types (shadscale/Indian ricegrass and greasewood/Great Basin wildrye) and "increasers" in the mesic habitat types (Nevada bluegrass-sedge and quaking aspen).

Differential Response by Habitat Type

Rodent community responses to livestock grazing differed greatly by habitat type. In the driest habitats fewer individuals and species were captured in the livestock-grazed than -ungrazed communities. The chisel-toothed kangaroo rat, *Dipodomys microps,* was the only rodent found in the grazed shadscale/Indian ricegrass community and was captured in greater abundance there than in the ungrazed shadscale/Indian ricegrass community. Shadscale leaves comprise the bulk of the diet of this species (Johnson 1961). Populations of all species except the chisel-toothed kangaroo rat and deer mouse appeared to be reduced by livestock grazing in the greasewood/Great Basin wildrye communities.

The least chipmunk, Great Basin pocket mouse, and deer mouse were the most abundant rodents in livestock-grazed and -ungrazed sagebrush-dominated

TABLE 4. Number of Animals Captured, Number of Species, and Shannon Indices of Livestock-grazed and -ungrazed Communities (grazed/ungrazed).

Species	Shadscale/ Indian ricegrass	Greasewood/ Great Basin wildrye	Low sage/ Idaho fescue	Big sage/ bluebunch wheatgrass- Thurber needlegrass	Big sage/ Idaho fescue	Nevada bluegrass- sedge	Aspen	Total
Spermophilus townsendi	–	–	–	–	–	1/0	–	1/0
Spermophilus lateralis	–	–	–	–	–	–	4/0	4/0
Ammospermophilus leucurus	–	1/4	–	–	–	–	–	1/4
Eutamias minimus	0/2	0/4	0/9	5/11	33/8	13/0	1/0	52/34
Eutamias amoenus	–	–	–	–	–	–	0/2	0/2
Perognathus longimembris	0/2	0/9	–	–	–	–	–	0/11
Perognathus parvus	0/1	–	6/19	4/6	–	6/0	2/0	18/26
Microdipodops megacephalus	–	1/0	–	–	–	1/0	–	2/0
Dipodomys ordi	–	–	–	–	–	3/0	–	3/0
Dipodomys microps	5/3	4/4	–	–	–	–	–	9/7
Dipodomys heermanni	–	–	1/0	–	–	–	6/0	6/0
Reithrodontomys megalotis	–	1/8	–	–	–	–	–	2/8
Peromyscus maniculatus	0/3	10/2	3/16	18/14	26/26	11/4	52/33	120/98
Onychomys leucogaster	–	–	–	–	–	1/0	–	1/0
Neotoma lepida	–	0/4	–	–	–	–	–	0/4
Microtus montanus	–	–	–	0/1	–	0/76	–	0/77
Microtus longicaudus	–	–	–	0/4	–	–	0/14	0/18
Lagurus curtatus	–	–	0/5	0/4	1/2	1/0	–	2/11
Zapus princeps	–	–	–	–	–	–	0/2	0/2
TOTAL	5/11	17/35	10/49	27/40	60/36	37/80	65/51	221/302
Number of species	1/5	5/7	3/4	3/6	3/3	8/2	5/4	
Shannon index of diversity (H')	.000/.672	.501/.800	.390/.555	.376/.677	.330/.317	.702/.086	.322/.387	

habitat types. Whereas the numbers of individuals and species captured were fewer in the grazed than ungrazed low sage/Idaho fescue and big sage/bluebunch wheatgrass-Thurber needlegrass communities, approximately 67% more animals were captured in the grazed than ungrazed big sage/Idaho fescue habitat. Greatest effects on species composition of these rodent communities were on the microtine rodents, which were apparently absent (or greatly reduced) in the grazed communities. The least chipmunk, Great Basin pocket mouse, and deer mouse were much less affected. The least chipmunk was approximately four times more abundant in the grazed than ungrazed big sage/Idaho fescue communities.

Livestock-grazed Nevada bluegrass-sedge and aspen communities were characterized by invasion of rodent species from the more xeric, shrub-dominated habitats. This was particularly evident in the wet meadow (Nevada bluegrass-sedge) community. Species such as the least chipmunk, heteromyid rodents (*Perognathus* spp., *Microdipodops megacephalus,* and *Dipodomys* spp.) and deer mouse acted as "increasers" with livestock grazing in these mesic habitats. Microtine rodents were the greatest "decreasers", the montane vole in the Nevada bluegrass-sedge communities and the long-tailed vole in the aspen communities.

Rodent Community Diversity

Rodent community diversity differences between livestock-grazed and -ungrazed habitats paralleled differences in plant life form diversity. Decreased plant life form diversity was associated with decreased rodent community diversity, and increased plant life form diversity was associated with increased rodent community diversity (Figure 1, the aspen habitat type has been left out of this analysis because the dominance of the trees masks the differences in understory vegetation for these data).

Percentage change in plant life form diversity accounted for approximately 79% of the variation in percentage change in rodent community diversity (H') ($r^2 = 0.785$). When the components of the Shannon index (species richness and evenness) are analyzed separately, it can be seen that both components responded similarly (Figure 1; none of the three regressions differ significantly, $P < 0.05$, from each other). Correlations between percentage change in plant life form diversity and percentage change in rodent species richness and evenness were very highly significant ($P < 0.001$), even when the regressions were forced through the origin as in Figure 1. Approximately 89% of the variation in change in rodent species richness ($r^2 = 0.888$) and 97% of the variation in change in evenness ($r^2 = 0.972$) was accounted for by percentage change in plant life form diversity.

It therefore appears that livestock grazing has reduced rodent species diversity in the drier communities and increased rodent species diversity in the more mesic communities in our study area. Diversity of plant life forms appears to be an important factor determining the diversity of rodent communities in these habitats.
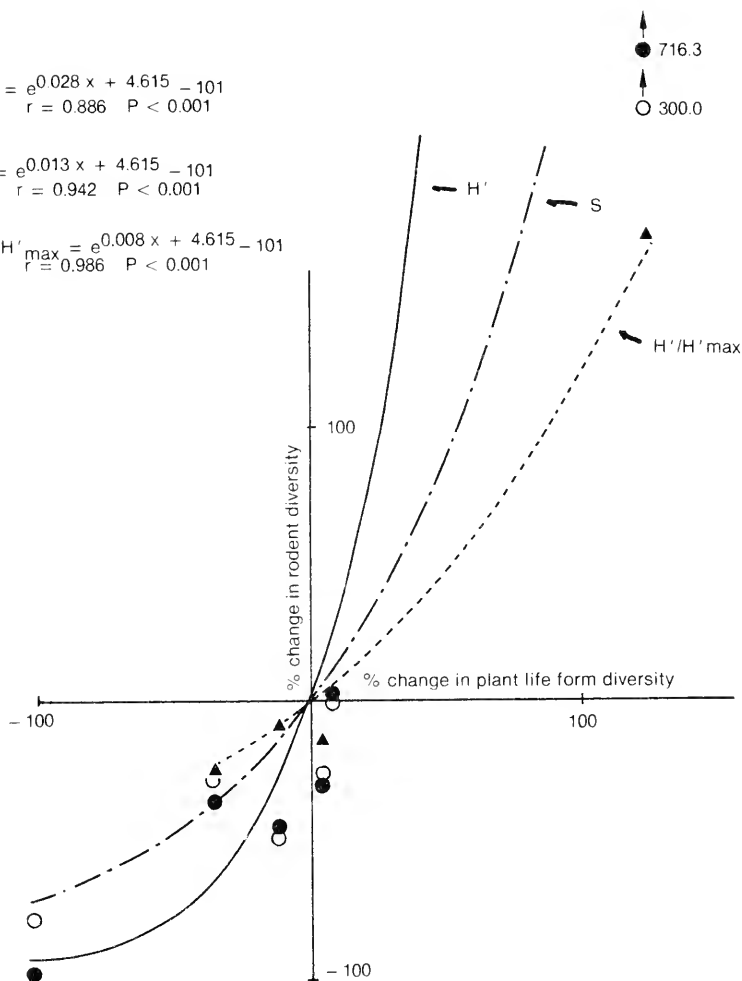
FIGURE 1. Relationships between percentage change in plant life form diversity (from "potential" to "present" conditions) and percentage change in rodent community diversity parameters. H' = Shannon's index of diversity, S = species richness, H'/H'$_{max}$ = species evenness. Regressions have been forced through the origin. Rodent diversity parameters were coded by addition of the constant 101 to enable calculation of the exponential equations.

CONCLUSIONS

Livestock use in the study area has resulted in a marked decreased relative abundance of perennial herbs, particularly bunchgrasses, in all habitat types analyzed. This has had differential effects on plant and animal community structure, however, and these effects appear to be predictable on the basis of soil moisture relationships.

The most xeric habitat types are potentially dominated by shrubs, with lesser amounts of grasses and forbs. Reduction of herbaceous vegetation by livestock

grazing therefore results in a reduction in plant life form diversity in these communities. On the other hand, the most mesic habitat types are potentially dominated by herbaceous vegetation, with lesser amounts of shrubby species. Reduction of herbaceous vegetation and concomitant increased abundance of shrubs as a result of livestock grazing results in an increase in plant life form diversity (up to a point) in these communities. Habitat types intermediate between these extremes respond similarly.

Reduced relative abundance of herbaceous vegetation results in differential effects on rodent populations. Some species consistently appear to react as "decreasers" with livestock grazing. These are species dependent upon herbs, particularly grasses, for both food and cover and are exemplified by the microtine rodents. Other species may react as "decreasers" in xeric habitats and "increasers" in mesic habitats. This kind of response was demonstrated by the least chipmunk, Great Basin pocket mouse, and deer mouse. Statements such as "range depletion favors an increase in deer mice populations" (Larrison and Johnson 1973:262; also see Phillips 1936), therefore, may not be appropriate in many instances.

The differential effects of livestock on plant life form diversity had parallel effects on rodent community diversity in this study. Reduced diversity of plant life forms in the xeric habitats was associated with reduced rodent diversity; increased diversity of plant life forms in the mesic habitats was associated with increased rodent diversity. These relationships were true for both rodent species richness and evenness.

Increased plant life form diversity probably increases the diversity of seed size and microhabitat as well as other factors, such as seed type and possibly resource predictability. Resource predictability may increase for an opportunistic forager, since different plant life forms tend to exploit different soil moisture resources (Solbrig and Orians 1977) and, thus, are not all similarly affected by climatic variability. In this respect, it is important to note that the greatest increases demonstrated by rodent species in the present study were by opportunistic (generalist) granivorous foragers—least chipmunk, Great Basin pocket mouse, and deer mouse. Thus, an increase in diversity of plant life forms probably results in an increase in several resource axes potentially suitable for partitioning—seed size, seed type, microhabitat, and interactions of any two or all three of these.

The relative composition of plant life forms is a very general and, perhaps, superficial component of habitat structure. Nevertheless, it is often the most easily recognized feature of a landscape; and our data indicate that it is of ecologic significance to rodents. We do not believe that the differences in rodent populations of our livestock-grazed and -ungrazed communities were related solely to differences in plant life form composition, but we do suggest that rodent communities respond to a complex of habitat changes identifiable over a wide range of habitat types by relative composition and diversity of plant life forms. The small sample sizes of only six or seven communities with comparative data and a total of 523 rodents captured limit the strength of this conclusion, however, and the relationship needs further verification.

We have examined livestock grazing effects on only one aspect of habitat quality. Equally (and perhaps more) important measures of habitat patchiness

and juxtaposition of patches, foliar structure, layering, plant species diversity, productivity, etc., remain to be investigated. Furthermore, we do not intend to imply that the observed influences on habitat structure are static. For example, whereas livestock grazing may initially increase diversity of plant life forms in grass-dominated habitats by creating a more even distribution of dominance among herbs and woody species, further excessive livestock use may reduce plant life form diversity by further reduction (or elimination) of the herbaceous species. We have considered rodent diversity only *within* habitat types, not over the landscape as a whole. While livestock use may result in an increased rodent diversity within meadows, for example, this may result in a reduction in rodent diversity over the landscape as a whole due to the increased similarity of the meadows with the more widespread shrub-grass habitat types.

Historically, livestock grazing-induced changes in habitat structure are a very new type of disturbance to Great Basin communities. The effects must be recognized for an accurate interpretation of plant and animal community relationships, particularly in studies dealing with community structure, species packing, and evolutionary relationships.

Our data are of an extensive nature, but they do provide some insight into the influence of livestock grazing on a variety of types of vertebrate habitat in the Great Basin. They underscore the importance of assessing grazing impact on a "habitat type" basis, that is, assessing current conditions in relation to potential conditions and recognizing the different potentials of different biotic communities.

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INTERTIDAL VERTICAL DISTRIBUTION AND DIETS OF FIVE SPECIES OF CENTRAL CALIFORNIA STICHAEOID FISHES [1]

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Cebidichthys violaceus, Anoplarchus purpurescens, Xiphister atropurpureus, Xiphister mucosus, and *Xererpes fucorum,* were found to differ in their intertidal distribution and food habits. Analysis of 15 transects revealed *C. violaceus* and *X. mucosus* to be distributed throughout the entire vertical range sampled, while *X. atropurpureus, A. purpurescens,* and *Xer. fucorum* were found to be concentrated in the lower half of the transects closer to the shoreline. Both *C. violaceus* and *X. mucosus* were differentially distributed according to size, with smaller individuals living higher in the intertidal zone. Analysis of gut contents revealed *A. purpurescens, X. atropurpureus,* and *Xer. fucorum* to be mainly carnivorous, while *X. mucosus* and *C. violaceus* were found to be chiefly herbivorous. Carnivorous species had gut lengths approximating 50% of the total body length, whereas herbivores had gut lengths approaching 100% of total body length. Differences in distribution and food habits are assumed to be mechanisms facilitating coexistence of these five morphologically and ecologically similar species.

INTRODUCTION

Studies on the ecology of intertidal organisms generally emphasize distribution and dynamics of sessile species with limited mobility with little or no reference to fishes. In the eastern North Pacific, several teleostean families inhabit the intertidal zone yet very little is known of their ecology. Members of the intertidally occurring fish families Stichaeidae and Pholididae are remarkable in their ability to withstand exposure to atmospheric conditions for considerable lengths of time (Hubbs 1941; Horn and Riegle in press). At low tide, these fishes take refuge in tidepools, beneath stones and boulders and in damp vegetation, thus exposing themselves to atmospheric conditions until re-immersion by the advancing tide. The purpose of this study was to determine the intertidal vertical distribution and food habits of five species of stichaeoid fishes. The species studied, *Anoplarchus purpurescens, Cebidichthys violaceus, Xiphister atropurpureus,* and *Xiphister mucosus* of the family Stichaeidae and *Xererpes fucorum* of the family Pholididae, are the stichaeoids most commonly encountered in the intertidal zone of central California.

METHODS

The study area was located within a 2-km stretch of rocky beach 3 to 5 km south of the Piedras Blancas Light Station, San Luis Obispo Co., California (lat 35° 40' N, long 121° 17' W.). The coastline runs in an east-west direction which, together with numerous rock outcroppings and kelp beds just offshore, serve to protect the area from excessive turbulence, particularly from swells from the north. The substrate consists of rock reefs dispersed among broad mud, cobble,

and sand beaches. The rocky bottom extends into the subtidal region and has a well-defined zone of interface with the sandy beach of the upper intertidal region.

Determination of Vertical Distribution

The vertical distribution of each of the five species of stichaeoids was determined from five transects taken during low tide periods through the exposed rocky shore at each of three different sites in the study area from May 1972 to January 1973. Transect sampling was done on days of greatest exposure of intertidal substrates at low tides. Most sampling was done when low tides were at least −1.0 ft below mean lower low water (MLLW).

Site 1 (5.0 km south of the Piedras Blancas Light Station) was partially enclosed at the northwestern edge by a large reef exposed at low tide and afforded the greatest degree of wave protection of all three sites. Site 2 (3.5 km south of the light station) was in a more exposed locale but had the aforementioned offshore rocks and kelp beds to absorb much of the shock of the incoming waves. Sites 1 and 2 had similar substrates composed of patches of muddy sand, loose cobble, large and small boulders interspersed with shallow pools and surfgrass beds. Site 3, the northernmost site (3.0 km south of the light station), was situated in a small shallow cove and was more exposed to incoming swells than either sites 1 or 2. The substrate at this site consisted of a solid rock base characterized by increasingly dense vegetation lower in the intertidal zone and several tidepools of varying depth and surface area.

Each transect consisted of six approximately equidistant square sample quadrats 2.25 m² in size. The first quadrat (Station 1) was at the water's edge at the lowest point of the low tide of the day the transect was taken. The last and highest quadrat, Station 6, was located at or near the zone of interface of the rocky and sandy parts of the beach. The length of each transect from the upper edge of Station 6 to the waterline was recorded; the other five stations were placed at equal intervals along the transect. Height of each quadrat station above MLLW was determined by sighting through a spotting scope situated just above Station 6 to a stadium rod marked off in metres and held vertically at the center of each station quadrat. By adding the increasing increments of height to the height of the low tide, obtained from tide tables, an absolute measure of the station height was calculated.

Loose stones were removed from the station quadrats and fishes were collected with a dipnet. When the sample site partially or wholly included a pool, the contents of the entire pool were collected using rotenone applied in small quantities until fish were anesthetized. Fishes were preserved in 10% formalin and later their relative abundance and total lengths recorded to the nearest mm.

Twenty-five individuals of each species (50 for *Cebidichthys*) were collected from June through August 1972 for analysis of diet. The fishes were killed with a rotenone-seawater solution and a solution of 5% formalin injected into the gut. The total length (TL) of each specimen was recorded and the digestive tract, from esophagus to anus, was removed and the length measured to the nearest millimetre. Stomachs were opened with an incision and the contents flushed out and placed in vials containing 5% formalin. Plants were identified to genus. Because of the more advanced state of digestion of animal food items, these were identified only to class or order. A quantitative measure of diet was at-

tempted by comparison of dry weight of plant versus animal material in stomachs. In cases where dry weight analysis was not feasible due to the size of the food mass, relative comparison was determined by percent occurrence of individual food items.

RESULTS

Vertical Distribution

Three species, *Anoplarchus purpurescens, Xiphister atropurpureus,* and *Xererpes fucorum,* were concentrated in the lower stations of the transects, *Cebidichthys violaceus* was most abundant in the upper half of the transects and *Xiphister mucosus,* while slightly more abundant in the lower stations, was present in all transect stations (Figure 1).
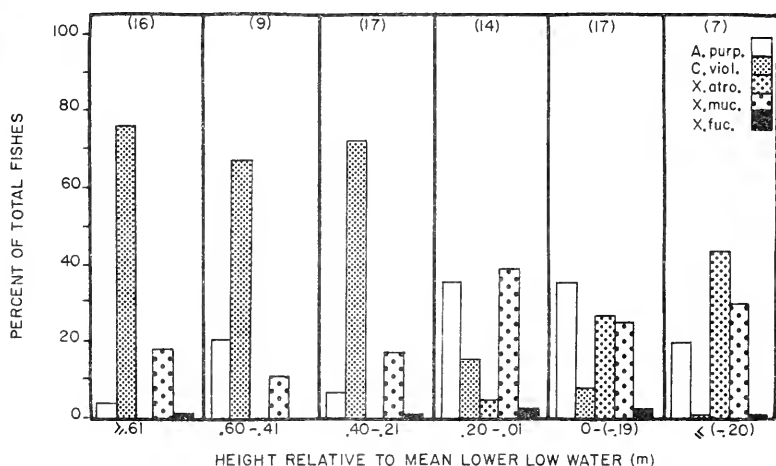

FIGURE 1. Percent composition of the five stichaeoid species at different intertidal height intervals, transect sites 1, 2, and 3 combined. The number of quadrats sampled in the indicated height interval is given in parentheses.

C. violaceus was the most abundant stichaeoid in the upper stations, comprising over 70% of the total sample above 0.21 m above MLLW. The correlation between fish size and height of occurrence in the intertidal zone was significant for both *C. violaceous* ($r = -0.761$) and *X. mucosus* ($r = -0.704$). *Xiphister atropurpureus* formed a substantial percentage of the sample in the lower transect stations below the zero tide level (Figure 1) and was never observed in Stations 5 or 6. *Anoplarchus,* like *X. mucosus,* was most abundant in Station 2, just above the lowest sample station. Because of the paucity of *Xer. furocum* in transect collections, little can be said concerning its distribution except that it was most frequently encountered in transects through dense vegetation. Color phases of *Xererpes,* which enable the fish to match the intertidal flora, appear to reflect seasonal changes in algal standing crop and species composition (Burgess 1978).

Analysis of Stomach Contents and Variation of Gut Length

Although diet studies were limited to 150 individuals collected during the summer months, analysis of the stomach contents of the five species revealed considerable differences in the kinds and frequency of food items comprising their diets (Table 1, Figure 2). The two species of *Xiphister* exhibited striking differences in diet composition. Red and green algae formed the bulk of the ingested material in *X. mucosus,* whereas *X. atropurpureus* ate almost exclusively decapods, with only a small amount of algae. Crustaceans were also the main food item of *A. purpurescens,* although considerable quantities of annelids and mollusks were recorded. *Xer. fucorum* fed almost exclusively on copepods. The shift in food habits with size observed by Montgomery (1977) in *C. violaceous* was confirmed, with small (< 80 mm TL) individuals consuming mostly gamma-

TABLE 1.   Frequency of Occurrence of Food Items in the Stomachs of Each Species Reported as the Number of Individuals in Which the Indicated Item Appeared

	A. purp.	C. viol.[1]	C. viol.[2]	X. atro.	X. muc.	X. fuc.
Total no. individuals examined	25	25	25	25	25	25
PLANT						
Chlorophyta						
Ulva					4	11
Cladophora			2			1
Rhodophyta						
Gigartina		4	11	1		
Gelidium			6			
Rhodoglossum			4			1
Smithora		5	1	1	11	
Iridaea			5			
Plocamium					3	
Schzymenia			1			
Porphyra			1			
Polyneura			1			
Unidentified red		2	10			
Zosteraceae						
Phyllospadix	2				1	
ANIMAL						
Nemertinia						
Nemertean worms				1		
Annelida						
Polychaeta	10	1		1		
Mollusca						
Gastropoda	10			1		
Pelecypoda	1		2			
Arthropoda						
Copepoda		1				11
Isopoda				2		3
Amphipoda	11	9	6	6	1	3
Caridea			2			
Anomura	1		2	7		
Brachyura	3	1				
Eggs	6		1			
No food in gut		5	2	9	1	11

[1] greater than 80 mm
[2] less than 80 mm

rid amphipods and large (> 80 mm TL) individuals consuming mostly algae (Table 1). The small food mass recovered in *C. violaceus* smaller than 80 mm and in *Xer. fucorum* prevented dry weight analysis. Although different methods of analysis were used in comparing the diets of large and small *Cebidichthys*, the strong differences appear to make such comparisons valid. Dry weight analysis, used for distinguishing relative percent abundance of plant and animal material, was not necessary with the exclusively carnivorous *A. purpurescens* and *Xer. fucorum*.

The carnivorous species, *A. purpurescens*, *X. atropurpureus*, *Xer. fucorum*, and *C. violaceus* (< 80 mm TL), had gut to total length ratios (GTR) of approximately 0.5, whereas herbivorous species *X. mucosus* and *C. violaceus* (> 80 mm TL), had gut to total length ratios closer to 1.0 (Figure 2). The most profound differences in diet and associated gut morphology were detected in the two closely related species of *Xiphister*. The range of GTR overlapped only slightly in these two species (Figure 2, 3). The GTR ranges were similar for *A. purpurescens* and *Xer. fucorum*, and *C. violaceus* had the greatest range of GTR owing to the disproportionate increase in gut length with increasing size and corre-
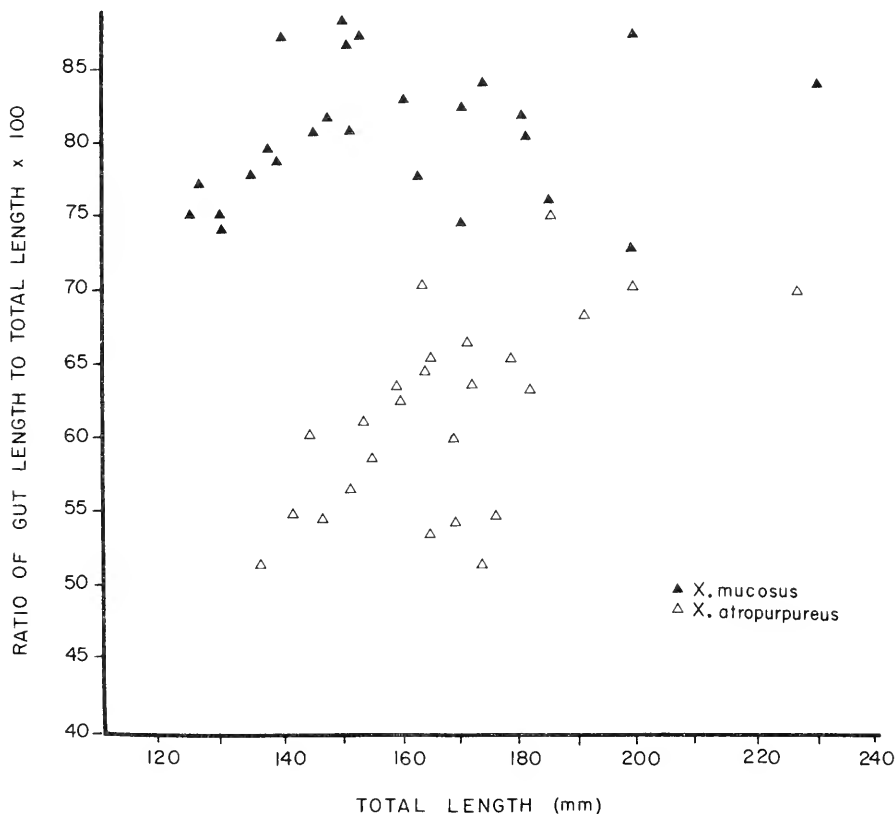

FIGURE 2.   Scatter diagram of gut-to-total length ratio (GTR x 100) versus total length for 25 specimens each of *X. atropurpureus* and *X. mucosus*.

sponding change in diet. A sharp increase in GTR was observed in the 70–80 mm TL range. This closely corresponded to the shift from carnivorous tendencies to herbivorous ones. A close relationship between food habits and relative gut length thus exists both among species and, in the case of *C. violaceus*, within species.
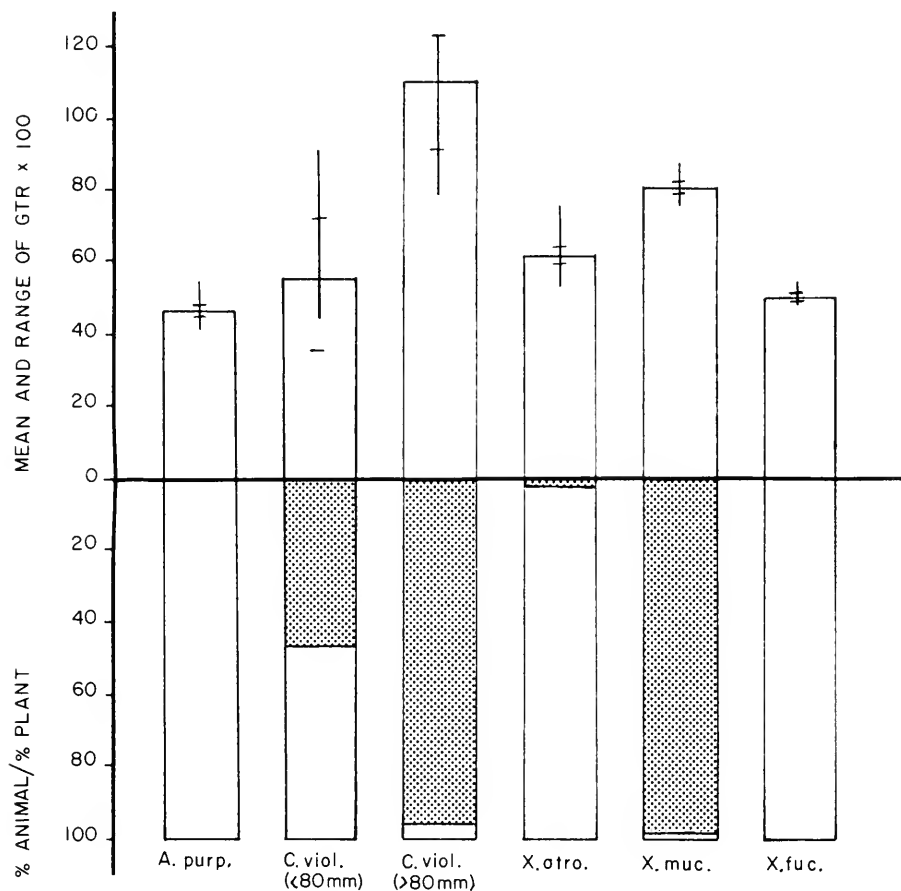

FIGURE 3.   Gut-to-total length ratio (GTR) (upper bars) and the relative percentage of plant and animal material consumed (lower bars) for each of the five stichaeoid species. Top of the upper bars represents mean GTR and vertical line represents range. Short horizontal bars are the 95% confidence intervals. Stippled portion of lower bars represents percent plant material consumed; blank portion represents animal material consumed.

DISCUSSION

In the eastern North Pacific the occurrence of low tides in early or late hours of the day and the prevalence of coastal fogs serve to minimize differences between atmospheric and oceanic conditions. Such uniformity may contribute to a comparatively large number of intertidal fish species, whose coexistence is possibly facilitated by partitioning of habitat and food resources. Studies indicate

a trend for related intertidal fishes to occupy different zones between the tide-marks (Williams 1954; Gosline 1965; Gibson 1969).

Miles' (1918) observations that the composition of blennioid species taken more than 1 m below the lowest tide was different than those found higher can only be verified with more intensive subtidal sampling. My study indicates that the five most common species of stichaeoid fishes of central California differ in the height to which they occur in the intertidal zone; studies on the subtidal ecology of these species may reveal differences in their subtidal depth ranges as well. Differential distribution within species is indicated by the presence of juvenile *Cebidichthys violaceus* and *Xiphister mucosus* in small pools high in the intertidal zone, while adults of the larger sticheoid species, such as *C. violaceus* (which may exceed 750 mm in length) and *X. mucosus* (which approaches 550 mm TL) tended to concenrate in larger, deeper pools and under rocks lower in intertidal zone.

While available habitat and food resources may influence intertidal distribution, other studies have shown the importance of physical factors, specifically temperature, in governing the distribution of cottids (Nakamura 1976) and stichaeoids (Barton 1978).

The abundance and variety of food available in the intertidal zone is paralleled by the high diversity of feeding types among the resident ichthyofauna (Gibson 1969), but little data exist on the food habits of the stichaeoids. Nakamura (1971) claimed that food is not a limiting factor in the complex and diverse intertidal environment, but the presence of a variety of feeding strategies among the stichaeoids suggests that food resources are sufficiently limited to promote the evolution of mechanisms partitioning these resources. Makushok (1958) claimed that the large majority of stichaeoids fed on small invertebrates, whereas Hubbs (1927) associated the loss of pyloric caeca in pholidids with the adoption of carnivorous habits. Stichaeoids, with their well developed caeca, were assumed by Hubbs to be vegetarians. Johnson (1954), Makushok (1958), and Wourms and Evans (1974) all noted the presence of algae in the gut of *X. atropurpureus*. However, the results of the present study showed that, in *X. atropurpureus,* the consumption of algae is incidental as this species has a marked preference for animals, while *X. mucosus* feeds chiefly on vegetation. While Gibson (1968, 1972) observed that sessile, encrusting organisms comprise a large portion of the diet of carnivorous intertidal fishes, the stichaeoids studied here showed an exclusive preference for free-living animals. While differences in carnivorous food habits among the stichaeoids may, as Mitchell (1953), Stephens *et al.* (1970), Nakamura (1971) pointed out, be the result of differences in habitat, the different food habits of the species of *Xiphister* indicate that closely related species, in broadly overlapping microhabitats, may have distinctly different feeding strategies. That these two species share the same microhabitat was repeatedly verified by observation of several individuals of both species under the same rock or in the same tidepool.

Differences in the ratio of gut length to total length in the two species of *Xiphister* suggest a functional relationship between gut length and food habits. Changes in food habits with age, either from carnivore to herbivore as in *Girella nigricans* (Mitchell 1953) and *Cebidichthys violaceus* (Montgomery 1977 this study), or from small animals to larger ones as in *Ulvaria subbifurcata* (LeDrew

and Green 1975) and *Gobius cobitus* (Gibson 1970), are well documented in intertidal fishes; but, the functional significance of change in gut length remains to be studied. The general observation (Lagler, Bardach, and Miller 1962) of longer gut in herbivores and the more recent observations (Stickney and Shumway 1974) of cellulase activity in a number of inshore fish species tend to support the conclusion that differences in gut to total length ratio between species, as in *Xiphister*, or within species, as in *Cebidichthys*, represent morphological and/or physiological accommodations to differing food habits. The GTR relates external morphological features (body length) with internal features (gut length). In the case of the stichaeoid fishes with a similar body morphology, differences in the calculated GTR are representative of differences in food habits. It would be inappropriate to attempt to relate the calculated GTR's of the elongate stichaeoids to unrelated species with distinctly different body morphologies such as deep bodied fishes.

The observed differences in diets, together with differences in intertidal vertical distribution, may facilitate the coexistence of several species of morphologically and ecologically similar species. The extent of the differences in diets must await a more detailed analysis of any seasonal trends in the abundance of the food items and of the foraging locations of the fishes. The extent of digestion and assimilation of plant material in herbivorous species, such as *Xiphister mucosus* and *Cebidichthys violaceus*, can only be determined by analysis of the physiological processes accompanying food consumption and digestion. The role of the stichaeoids as prey species in the inshore food chain needs to be assessed as well. Predation on intertidal populations, which in some blennioids accounts for up to 50% of the mortality (Stephens *et al.* 1970), may contribute generally to the maintenance of high species diversity (Paine 1966) and specifically to the coexistence of the five stichaeoid species in central California.

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SIGHTINGS OF CETACEANS IN THE GULF OF THE FARALLONES, CALIFORNIA, 1971–1979 [1]

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Census of cetaceans along a fixed 48-km transect between the Golden Gate Bridge, San Francisco, and Southeast Farallon Island, California, were conducted between 1971 and 1979. Six species (harbor porpoise, Dall's porpoise, Pacific white-sided dolphin, killer whale, California gray whale, and humpback whale were sighted on 93 of 263 censuses during the 107-month period; most frequently seen was the harbor porpoise. Weather and vessel characteristics affected results significantly; observer variation was not tested, but only a few observers were involved.

INTRODUCTION

Many observations of marine mammals at sea have been contributed by people who "happened to be there", primarily fishermen and whalers. In more recent times observations of a more systematic nature have been initiated, including the placement by various agencies of trained observers onto available vessels. As a result more and more information is being gathered on cetacean distribution and abundance. Many of these "platforms of opportunity", however, are only available seasonally or do not regularly follow the same cruise tracks, and thus the information becomes difficult to compare from year to year. Furthermore, the effect of the vessel on census results is rarely considered in analyzing data. From 1971 to 1979, biologists from the Point Reyes Bird Observatory (PRBO) censused marine birds and mammals along a fixed transect in the Gulf of the Farallones, California. The consistency in route traveled and in observers participating helps to overcome some of the problems associated with data gathered on "platforms of opportunity".

METHODS AND STUDY AREA

Cetaceans were counted along a transect between the Golden Gate Bridge, San Francisco and Southeast Farallon Island, 48 km to the west, from April 1971 to December 1979. During the 107-month period, 263 censuses were conducted under various weather conditions using both power and sailboats (Table 1). Each cruise lasted about 4 h each way. Fewer transects between October and March reflect the greater frequency of storms, resulting in more cancelled cruises. The study area (Figure 1) was divided naturally by the boundary between San Francisco Bay water and ocean water, marked by a distinct change in water color. This change occurred near the San Francisco Bay Entrance Buoy (SFBEB) approximately 22 km west of the Golden Gate Bridge, but exact location of the Bay water boundary varied according to tide and the strength of seasonal freshwater runoff. In general, east of the buoy waters were shallow and were heavily influenced by runoff; west of it waters were deeper (15–30 fm) and were influenced more by the California Current. This current exhibited three distinct phases during the year, evidenced in the water temperatures measured

at intervals along the cruise track: the upwelling period of strong northwest winds and cold, productive waters from February or March to July; the oceanic period of warm waters from August to November; and the Davidson Current period of moderately warm temperatures and extensive freshwater runoff from November to February (Bolin and Abbott 1963). During the upwelling period, temperatures were as much as 3.9°C colder west of the Bay water boundary, but during the remainder of the year temperature gradients were less extreme.
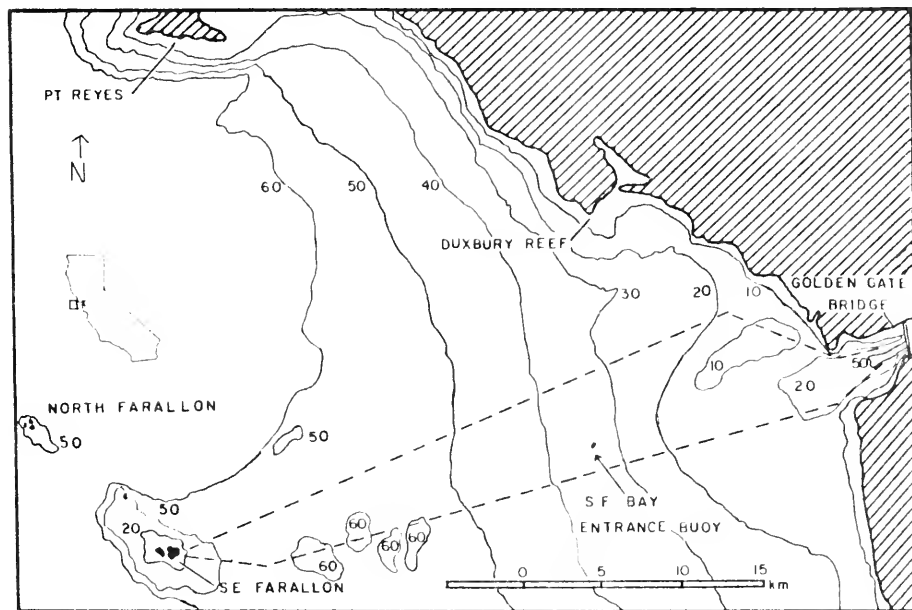

FIGURE 1.   The Gulf of the Farallones: study area for censuses between Southeast Farallon Island and the Golden Gate Bridge, San Francisco, California is marked by dotted lines; water depth in metres (2 m = approximately 1 fm).

SPECIES ACCOUNTS
Harbor Porpoise *(Phocoena phocoena)*

The harbor porpoise ranges from Morro Bay, California, north to Pt. Barrow, Alaska, but is uncommon south of Monterey Bay (Norris and Prescott 1961; Leatherwood, Evans, and Rice 1972). It is considered to be a porpoise of bays and inlets although some inshore (summer) to offshore (winter) migration does occur in the northwest Atlantic (Gaskin, Arnold, and Blair 1974). It is not known if such movements take place in the northeast Pacific. Little is known of the population size or of breeding areas of California; Morejohn (1977) indicated that parturition occurs from January through July.

Past reports of this species in the San Francisco Bay area are sketchy. Scammon (1874) reported it occasionally caught by fishermen in the Bay. More

TABLE 1. Cetacean Transects in the Gulf of the Farallones 1971–1979 (Number of Transects With Cetacean Sightings/Total Number of Transects).

						Months							
	J	F	M	A	M	J	J	A	S	O	N	D	TOTALS
1971				0/1	0/3	0/2	0/2	1/2	0/3	1/2	0/1	0/2	2/18
1972	2/4	0/2	0/3	0/1	0/5	3/5	2/5	0/4	0/4	0/3	0/2	1/3	8/41
1973	0/2	0/2	2/2	0/2	0/2	1/2	2/3	2/3	2/3	*	*	1/2	10/23
1974	*	1/1	1/1	1/2	0/3	1/2	0/1	*	1/3	*	*	*	5/13
1975	*	*	*	0/2	1/1	2/3	1/4	1/4	0/2	1/3	*	0/1	6/20
1976	*	*	2/3	0/2	2/5	1/4	2/5	0/3	1/5	0/2	0/1	1/3	9/33
1977	2/2	*	0/1	1/2	0/2	2/3	2/3	3/6	2/4	0/2	0/6	1/1	13/32
1978	*	*	*	1/2	1/4	4/6	3/5	1/5	1/3	1/4	1/4	2/6	14/39
1979	1/1	3/4	3/3	4/6	1/3	5/8	5/5	2/6	2/4	*	0/3	0/1	26/44
TOTALS	5/9	4/9	8/13	6/20	5/28	19/35	17/33	10/33	9/31	3/16	1/17	6/19	

* Census cancelled

recently, Brownell (1964) reported the harbor porpoise as "not common" in the Bay and suggested that its apparent decline could be due to increased pollution and boat traffic. During our study we saw only one inside San Francisco Bay (on 27 July 1975, off Ft. Baker), although it was the most frequently sighted cetacean outside the Bay. A subadult female was stranded alive on Angel Island, inside the Bay, on 7 July 1977 (M. Webber, Tiburon Environmental Center, pers. commun.).

In the Gulf of the Farallones we sighted harbor porpoise 55 times in groups ranging in size from 1 to 15 animals (mean pod size = 2). Although they were difficult to detect because they occurred in such small pods, spent little time at the surface, and did not approach boats or ride the bow wave, we saw them more frequently than any other cetacean. Most sightings were between April and August, the cold water upwelling period. All but one sighting during the October to March period occurred during the winter of 1978–79 when water temperatures were cooler than usual (measured at Southeast Farallon Island; PRBO unpubl. data). We saw harbor porpoise primarily in the deeper water west of the SFBEB. Earlier accounts described the species as being "common" in the shallower water east of the buoy (Brownell 1964; Fiscus and Niggol 1965), but only a third of our sightings were in these waters. Harbor porpoises are known to occur as far as 25–50 km offshore in Washington (Scheffer and Slipp 1948).

Dall's Porpoise *(Phocoenoides dalli)*

Dall's porpoise are found in waters from Alaska south to Baja California, although a large part of the population moves south in the winter and north in the summer (Leatherwood, Evans, and Rice 1972). They generally occur in deep waters: 91% (10/11) of Brownell's (1964) sightings were in waters deeper than 50 fm, and Fiscus and Niggol (1965) found few where waters were shallower than 100 fm except near the Farallones. Since a common prey of the Dall's porpoise is Pacific whiting *Merluccius productus,* (Scheffer 1953, Norris and Prescott 1961, Fiscus 1979, Morejohn 1979), their attraction to the Farallon area could be to feed on the whiting which is seasonally abundant there, as do California sea lions, *Zalophus californianus,* (Ainley, Huber, and Bailey, in press).

All but one of our sightings of Dall's porpoise were in the relatively deeper waters (15 to 30 fm) west of the SFBEB. One sighting of 10 animals, however, was close to shore, 4–5 km west of Duxbury Reef in waters 12–15 fm deep.

Most of the 29 sightings were in June and July; counts ranged from 1–15 animals (mean pod size = 6). This was the second most frequently sighted cetacean, although their behavior of splashing on the surface, "porpoising" and riding the bow waves makes them far more conspicuous than the harbor porpoise.

Pacific White-sided Dolphin *(Lagenorynchus obliquidens)*

The Pacific white-sided dolphin occurs from the Gulf of Alaska to Baja California (Leatherwood, Evans, and Rice 1972). We sighted it only once, a pod of 6 on 9 June 1974, 8 km west of the SFBEB.

Unidentified Porpoise

Porpoise could not be identified on 19 occasions. Four sightings east of the SFBEB were probably all harbor porpoise because of the tendency of that species to inhabit shallower water. A pod of 25–100 animals seen on 29 March 1973 was probably another species, because harbor porpoise do not gather in such concentrations (Norris and Prescott 1961, Morejohn 1977). The remainder of sightings was scattered throughout the year, with the majority occurring in the summer.

California Gray Whale *(Eschrictius robustus)*

Gray whales range from their winter breeding grounds in Baja California north to their summer feeding areas in the Arctic (Leatherwood, Evans, and Rice 1972). They are commonly observed along the California coast during both north and southward migrations.

Gray whales were seen 23 times on our transects, primarily in December and January during their southward migration and in February and March during the northward migration (Table 2). Sightings in May and June 1976 may have been (an) individual(s) summering in the area. Since 1972, up to 5 gray whales have spent at least part of the summer near the Farallones (Huber *et al.* 1979) rather than moving immediately to their more northerly feeding grounds.

TABLE 2. The Number of Cetaceans and Pods Sighted Per Cruise By Month.

					Month							
	J	F	M	A	M	J	J	A	S	O	N	D
Harbor porpoise												
individuals/cruise		0.2	0.2	0.3	0.4	1.2	0.5	0.3	0.7		0.5	0.3
pods/cruise		0.1	0.1	0.2	0.1	0.5	0.3	0.2	0.4		0.1	0.1
Dall's porpoise												
individuals/cruise		0.9			0.1	1.6	2.4	0.2	0.1	0.6		0.2
pods/cruise		0.1			0.1	0.3	0.4	0.1	<0.1	0.1		0.1
Pacific white-sided dolphin												
individuals/cruise					0.2							
pods/cruise					<0.1							
Gray whale												
individuals/cruise	1.6	0.7	0.8	0.3	<0.1	<0.1						0.5
pods/cruise	0.6	0.3	0.4	0.2	<0.1	<0.1						0.2
Humpback whale												
individuals/cruise									0.1			
pods/cruise									0.1			
Killer whale												
individuals/cruise						<0.1		0.1				
pods/cruise						<0.1	<0.1					

Most gray whales were west of the SFBEB travelling in a north-south direction. In spring 1979 several small individuals close to the Golden Gate Bridge may have been juveniles migrating north. Recently researchers have found that juveniles and cows with calves migrate north much closer to shore than previously believed (Baldridge 1974). All gray whales seen were single animals or in small pods of 2–6 animals (mean pod size = 2). In addition, unidentified large whales

were sighted on four occasions, December to March. It is likely these were also gray whales.

Killer Whale (*Orcinus orca*)

Killer whales are found in all oceans (Rice 1977) and probably breed throughout their range in the Pacific (Morejohn 1977). Two were seen 21 August 1971 feeding on a pinniped between Southeast Farallon and the SFBEB, and another individual was seen 28 June 1972 6 km east of the Island (Table 2).

One unidentified whale, possibly a pilot whale, *Globicephala melaena,* or a killer whale, was recorded 28 October 1978 near the Island.

Humpback Whale *(Megaptera novaengliae)*

We observed humpback whales on only one transect, although we have seen them regularly to the west from Southeast Farallon in the fall and, since 1977, in the spring (Huber *et al.* 1979). On 21 September 1974, two humpbacks were seen travelling south 10 km and 4 km east of the Island.

DISCUSSION

Several factors influence the interpretation of these censuses. Results were significantly affected by weather conditions and choice of vessel. The difference between the number of cetaceans seen under low, moderate, and high wind conditions was significant ($p < .05$; t-test). Under low wind conditions (0–7 kts) and calm seas, marine mammals were seen on nearly half of the cruises (57/126). As sea height increased with wind speed, it obscured visibility along the water surface so that we saw marine mammals on less than a third of the transects (32/106) under moderate wind conditions (8–15 kts) and on only four transects (4/31) when winds exceeded 15 kts. Higher winds also dispersed the blows and splashes of cetaceans more rapidly.

Other factors affecting the number of cetaceans observed were the type of vessel and its speed, both of which varied from census to census. In 1971 and 1972 almost all censuses were from U.S. Coast Guard cutters travelling at 15 kts. High speed, rather than an absence of animals, may account for the few mammals seen during this period (Table 1). Conversely, the increased number of sailboats and slower power boats travelling at 4–10 kts may account for increased sightings after 1973.

Under favorable (low) wind conditions, an observer was more likely to see marine mammals from a sailboat travelling 4–7 kts (32/55) than from a power boat traveling 8–10 kts (25/71), but the difference was not statistically significant ($p > .10$; x^2 test). However, significantly more harbor porpoises were seen from sailboats (38/58) than from power boats (20/58 ($p < .05$), probably due not only to the slower speed but also to the quieter engines.

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NOTES

RECORD OF THE STRIPED MULLET, *MUGIL CEPHALUS,* IN SAN FRANCISCO BAY, CALIFORNIA

On 5 November 1980, a striped mullet, *Mugil cephalus* Linnaeus, 43.5 cm SL, 49.0 cm FL and 2.12 kg body weight was collected by gill net at the National Marine Fisheries Service dock at Tiburon, California. The fish, a gravid female, was collected while sampling for striped bass, *Morone saxatilis.* This is the first record of a striped mullet in San Francisco Bay, although a *M. cephalus* larva was identified in the Sacramento-San Joaquin Delta (Quelvog 1977). The previous northern limit was listed by Miller and Lea (1972) as Monterey.

The identification of the specimen was verified by William N. Eschmeyer, California Academy of Sciences, Department of Ichthyology. The specimen is deposited at the Academy (CAS 47123).

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BOOK REVIEWS

The California Islands: Proceedings of a Multidisciplinary Symposium

Edited by Dennis M. Power; Santa Barbara Museum of Natural History; Santa Barbara, CA 93105; 1980; 787 p.; illustrated; $20.00.

The California Islands include 18 islands or island groups along the west coast of North America from the Farallon Islands west of San Francisco to Natividad Island off Point Eugenia, Baja, California. The purpose of the 1978 California Islands Symposium was to bring together researchers from several disciplines and to provide a means to summarize and advance knowledge of the California Islands and adjacent waters. This technical volume contains 43 papers from a diverse selection of topics presented at the symposium, although most primarily concentrate on one or more of the Channel Islands off the coast of southern California.

The papers of the Proceedings are organized by the editor into six major sections, not including the introduction and a summary. The first section treats general geologic history and contains a specific work on paleontology. This is followed by two papers discussing prehispanic man and his effects on island ecology. The next two sections concern botany, discussing vegetation changes, the impact of feral animals, and the evolution and ecology of land plants. Then there is a large section on biogeography, evolution, and ecology of marine organisms, including invertebrates, algae, fish, seabirds and pinnipeds. The last section concerns biogeography, evolution, and ecology of land animals, including general distribution and more specific works on amphibians, reptiles, birds, and mammals. In the summary, the editor compares the works of this symposium with research of the past. As stated in the introduction, "If one general theme can be derived from the collection of research papers in this book, it is that the physical and biological components of both land and sea are interwoven in often complex cause-and-effect relationships. For the California Islands, variation in size, shape, and degree of isolation coupled with variance in oceanographic and climatic setting, prepare the state for evolutionary changes and ecological interactions within the biota."

This volume is a useful reference source for biologists and others interested in almost any aspect of the natural history of the California Islands. It is well organized, and provides important documentation of the current state of California island research.—*Jan E. Bickett.*

ECOLOGY OF FRESHWATERS

By Brian Moss; Blackwell Scientific Publications, Great Britain, distributed by John Wiley and Sons, New York, 1980; 332 p. $27.95.

Ecology of Freshwaters is not a limnology book, but it should be required reading in every limnology course. The title of this British publication is accurate: the author's focus throughout the book is on the entire ecosystem in which a particular body of freshwater is found. He discusses the importance of the drainage basin, geographical location, i.e. latitude and altitude, atmosphere, and allochthonous material. He even brings up the point that non-aquatic vertebrates such as birds, mammals, and reptiles can considerably alter the structure of an aquatic ecosystem by predation or by increased nutrient loading through their excrement. The scope of the book is broad as he illustrates his subjects with examples from waters all over the world.

The book was aimed at undergraduates and graduate students just starting a project or career. For undergraduates every sentence brings important, new information. For graduates, and established professionals too, this book is a valuable reference as it contains a great deal of information on techniques, including new and uncommon procedures as well as problem areas. The style is extremely readable. The author even gives life to such perennially dry topics as chemical recycling in profundal sediments and nutrient cycling through the planktonic food web. His progression is logical as he continuously builds on previously laid foundation.

The last four chapters are devoted to how man modifies aquatic ecosystems. This includes discussions on fisheries, pollution, waste disposal, water supply, and conservation. By necessity these discussions are cursory, but as always, every chapter concludes with many references for further reading.

In his last chapter, on conservation, he states that freshwater habitats are some of the most vulnerable, and most likely to be altered by man in his constant attempt to "improve" upon nature. He concludes by stating that the biggest problem in trying to conserve freshwater, or indeed any ecosystem, often lies primarily within the realm of politics or social controversy.—*D. A. McGriff*

Resources Management and Environmental Uncertainty, Lessons from Coastal Upwelling Fisheries

By Michael H. Glantz and J. Dana Thompson; John Wiley & Sons, Inc., New York, 1981; 544 p. $42.50

Administrators, politicians, fishermen, fish processors, and sociologists as well as fisheries biologists, oceanographers, and meteorologists will find something to interest them in this book. Interest in the effects of natural oceanic and atmospheric phenomena has increased greatly during the past two decades. The obvious and great impact of one such phenomenon, El Niño, upon what was for a time the world's largest fishery, the Peruvian anchovy fishery, has probably had much to do with this increased interest in seeking to identify the oceanic and atmospheric parameters impacting similar fisheries.

This book brings together the knowledge and views of several of the most prominent investigators of environmental impacts upon these fisheries. Eighty percent of the book is about the Peruvian experience. The four other important upwelling regions of the world, western North America, northwest and southwest Africa, Somalia, and Arabia are discussed in variable degrees. The editors have drawn papers from a variety of disciplines as well as geographical areas. Socioeconomics, politics, and administration are given as much space as the natural sciences of meteorology, oceanography, and biology.

Michael Glantz's introduction provides a cohesive element often missing from multi-authored books, and the extensive list of references at the end of each chapter is especially valuable to those wishing to further investigate the subject of that chapter. J. Dana Thompson explains the relationship between wind, ocean currents, and the fish catches of upwelling regions in terms that anyone can understand whether or not they have had any natural science training. Two chapters describing Peru's anchoveta fishery were published previously. One by Gerald J. Paulik was first published in 1971; the other, by Robert Cushman Murphy in 1954, was previously available only in Spanish.

An excellent history of the struggle to control California's sardine fishery is written by John Radovich. David Cram similarly discusses the south African experience.

Three chapters are technical. Two will be of interest primarily to those wanting to familiarize themselves with hypothetical explanations of physical mechanisms behind El Niño events. While many readers will want to skip much of these technical chapters, familiarity with material in their abstracts and summaries will contribute to a full appreciation of later chapters. A very readable chapter on the economic history of the Peruvian anchoveta fishery contains much information relevant to other fish meal fisheries including California's anchovy fishery. The performance of two policy making systems; one with limited government involvement, the other with direct government administration, are compared in a chapter by Lynn A. Hammergren.

A 1969 report by Instituto del Mar del Peru calling for strict fishery control is reprinted. The report suggests methods for reducing fleet and processing plant capacities and discusses the anchoveta fishery's impact on birds.

The last three chapters conclude, for different reasons, that an El Niño forcast would either be of little benefit to the people of Peru or is ulikely to be achieved. Administrators and others who participate in deciding where our increasingly sparse fishery research dollars are to be spent should be very interested in these three final chapters.—*James E. Hardwick*

INSTRUCTIONS TO AUTHORS

EDITORIAL POLICY

The editorial staff will consider for publication original articles and notes dealing with the conservation of the fauna and flora of California and its adjacent ocean waters. Authors may submit two copies, each, of manuscript, tables, and figures for consideration at any time.

MANUSCRIPTS: Authors should refer to the *CBE Style Manual* (fourth edition) for general guidance in preparing their manuscripts. Some major points are given below.

1. *Typing*—All material submitted, including headings, footnotes, and references must be typewritten double-spaced on white bond paper. Papers shorter than 10 typewritten pages, including tables, should follow the format for notes.

2. *Citations.*—All citations should follow the name-and-year system. The "library style" will be followed in listing references.

3. *Abstracts*—Each paper will be introduced by a short, concise abstract. It should immediately follow the title and author's name and be indented at both margins to set it off from the body of the paper.

4. *Abbreviations and numerals*—Use approved abbreviations as listed in the *CBE Style Manual*. In all other cases spell out the entire word.

TABLES: Each table should be typewritten double-spaced throughout with the heading centered at the top. Number tables with arabic numerals and place them together in the manuscript following the references. Use only horizontal rules. See a recent issue of *California Fish and Game* for format.

FIGURES: Submit figures at least twice final size so they may be reduced for publication. Usable page size is 4⅝ inches by 7⅜ inches. All figures should be tailored to this proportion. Photographs should be submitted on glossy paper with strong contrasts. All figures should be identified with the author's name in the upper left corner and the figure number to the upper right corner. Markings on figures should be in blue pencil or grease pencil, as this color does not reproduce on copyfilm. Figure captions must be typed on a separate sheet headed by the title of the paper and the author's name.

PROOF AND REPRINTS: Galley proof will be sent to author's approximately 60 days before publication. Fifty reprints will be provided free of charge to authors. Additional copies may be ordered through the editor at the time the proof is submitted.